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PHYLOGENY OF THE CARDIIDAE (BIVALVIA): PHYLOGENETIC RELATIONSHIPS AND MORPHOLOGICAL EVOLUTION WITHIN THE SUBFAMILIES CLINOCARDIINAE, LYMNOCARDIINAE, FRAGINAE AND TRIDACNINAE

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ABSTRACT

The cardiid bivalve taxa *Plagiocardium, Maoricardium,* Clinocardiinae, Fraginae, *Goethemia,* Lymnocardiinae, and Tridacninae form a monophyletic group. The most parsimonious cladograms of this group have a topology of (*Plagiocardium* (*Maoricardium* (Clinocardiinae (Fraginae (*Goethemia* (Lymnocardiinae, Tridacninae)))))).

The giant clams form a subfamily (Tridacninae) of Cardiidae. In the ontogeny and phylogeny of giant clams, the morphology and position of the muscle scars and hinge changes from that resembling the dimyarian *Cerastoderma* to the monomyarian morphology displayed by *Hippopus* and *Tridacna,* which have lost the anterior half of the shell. This peramorphic trend is the result of differential growth: tremendous growth rate of the posterior portion of the shell and a zero or even negative growth rate of the anterior half of the shell.

All tridacnines and several species of fragines are known to harbor photosymbiotic zooxanthellae. These algae transfer excess carbon to its cardiid host. It is known that the chemosymbiotic lucinid and solemyid bivalves reduce or lose many features of their digestive systems. The sulfur-reducing bacteria in lucinids and solemyids provide most of the nutrients that the host clam needs, thus making a full digestive system unnecessary. Most fragine cardiids reduce numerous structures of their digestive systems. Only a few fragines have been examined for the presence of photosymbionts. Based upon their anatomy, it is predicted that most or all of the derived fragines harbor photosymbionts. Tridacnines harbor photosymbionts but do not appreciably reduce their digestive systems. The possession of both photosymbionts and a fully functional digestive system allows tridacnines to be the fastest growing and largest of the extant bivalves.

Key words: cardiids, giant clams, Fraginae, phylogenetics, heterochrony, paedomorphosis, peramorphosis, photosymbiosis.

INTRODUCTION

Bivalves of the family Cardiidae (cockles and giant clams) originated in the Late Triassic and have a present-day diversity of approximately two hundred species. Cardiids have been the subject of considerable taxonomic work by both paleontologists and malacologists, and numerous subfamilies, genera, and subgenera have been erected. However, few studies of the phylogenetic relationships amongst these taxa within the Cardiidae have been undertaken.

The only proposed phylogenies for the family Cardiidae are those of Kafanov & Popov (1977) and Schneider (1992). Kafanov & Popov based their phylogeny on two key character complexes: shell microstructure and morphology of the interior of the stomach. Schneider (1992) proposed a preliminary phylogenetic hypothesis for the Cardiidae based on a cladistic analysis of 54 characters of 36 taxa. In that analysis, at least one member from each of the subfamilies recognized by Kafanov & Popov (1977) and Keen (1951, 1969a, 1980) was included, as well as additional taxa of uncertain affinities. The representatives of the subfamilies Clinocardiinae, Fraginae, Tridacninae, and Lymnocardiinae were found to be a monophyletic group. The synapomorphies of this group were: (1) few tentacles, (2) oval shell shape during ontogeny, (3) shape of right anterior cardinal socket, (4) shape of right posterior cardinal tooth, (5) shape of right anterior cardinal tooth (characters and states listed in Schneider, 1993a).

MATERIALS AND METHODS

A cladistic analysis of 34 taxa and 51 characters with 140 character states was made

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using PAUP 3.1.1 (Swofford, 1993). There are 24 shell characters, 26 anatomical characters, and one periostracal character. Characters were coded from examination of specimens, unless otherwise indicated. The heuristic branch-swapping routine with random addition and tree-bisection reconnection options was used. The accelerated transformation option (ACCTRAN) was used, and steps were not added to terminal taxa with polymorphisms (Schneider [1995] explains these options.) The data matrix is presented in Table 1, and synapomorphies (shared derived characters) for one of the most parsimonious trees are presented in Table 2. With the exceptions of *Keenocardium, Maoricardium, Chametrachea*, *Trigoniocardia*, and *Hypanis (Monodacna),* data for each of the ingroup taxa are represented by the type species (Appendix 1). This has been termed the exemplar approach (Wheeler et al., 1993). Therefore, this analysis should be taken as a phylogeny for these species only, because character states presented may not be constant throughout all species of a given genus or subgenus. All Recent taxa were investigated anatomically, except for *Yagudinella.* Anatomical data for *Yagudinella* were taken from Kafanov (1980). Shells were examined for all taxa except *Fuscocardium*, for which data were taken from descriptions and illustrations in Oyama (1973). Missing data are coded by a question mark (?) in Table 1.

Fourty-nine of the 51 characters are unordered. Two characters, shell shape (32) and pseudocarina (41) are ordered on the basis of outgroup analysis and ontogeny. I follow Alberch's (1985) criterion for justification of the ordering of characters. Alberch argued that the only characters that can be ordered in a phylogenetic analysis are those in a casual sequence. That is, the state of a character at time 1 is dependent upon the state of that character at time 0; the state at time 2 depends upon the state at time 1, etc. Bivalves, given accretionary growth, fall under this strict criterion. The justifications for the ordering schemes of these characters are given in the character descriptions below.

Selection of Ingroup Taxa:

All genera and subgenera of the subfamilies Clinocardiinae, Fraginae, and Tridacninae are represented, along with three of the Recent genera of Lymnocardiinae.

For the subfamily Clinocardiinae, those taxa accepted by Kafanov & Popov (1977) and Kafanov (1980) are represented in the present analysis.

For the Fraginae, all taxa accepted by Keen (1969a, 1980) are represented, with the exception of *Afrocardium* (see below). Kafanov & Popov (1977) include a number of other taxa in Fraginae, such as *Parvicardium*, *Papillicardium, Plagiocardium,* and *Maoricardium.* These four taxa are represented in the analysis. Schneider (1992) found *Plagiocardium* and *Parvicardium* to be members of Fraginae. *Papillicardium* is usually taken to be either (1) a subgenus of *Parvicardium* (Keen, 1969a, 1980; Kafanov & Popov, 1977; Voskuil & Onverwagt, 1989), (2) a junior synonym of *Parvicardium* (Glibert & van de Poel, 1970; Popov, 1977; Lambiotte, 1979), or (3) a junior synonym of *Plagiocardium* (Spada & Della Bella, 1987). Marwick (1944) erected *Maoricardium* as a genus and considered its closest relatives to be *Clinocardium* and *Cerastoderma.* Marwick also thought that *Maoricardium* was extinct. Keen (1951, 1969a, 1980), Habe (1951), and Wilson & Stevenson (1977) classified *Maoricardium* as a subgenus of *Plagiocardium* and extended the former's range into the Recent. Popov (1977), Kafanov & Popov (1977), Beu & Maxwell (1990), and Voskuil & Onverwagt (1991) gave *Maoricardium* generic rank. Popov (1977) and Kafanov & Popov (1977) considered the Recent species placed in *Maoricardium* by Keen, Habe, and Wilson and Stevenson as belonging to *Plagiocardium.* For the present analysis, the Recent species in question are considered to belong to *Maoricardium* on the basis of shell shape and details of the cross-striae in the rib interspaces. *Maoricardium* is represented in the present analysis by the Recent species *Maoricardium pseudolatum* Voskuil & Onverwagt, 1991, for which anatomical specimens were available. Popov (1977) and Kafanov & Popov (1977) placed *Acanthocardia* and *Orthocardium* in Fraginae, but otherwise these taxa have been considered members of Cardiinae (Keen, 1951, 1969a, 1980; Nordsieck, 1969; Glibert & van de Poel, 1970, 1973; Meechan, 1987; Voskuil & Onverwagt, 1989). *Acanthocardia* and *Orthocardium* were found to be cardiines in my preliminary analysis (Schneider, 1992). Popov (1977) and Kafanov & Popov (1977) also considered *Schedocardia* and *Loxocardium* to be fragines. Keen (1951, 1969a, 1980) considered *Schedocardia* to be a subgenus of *Acanthocardia;* Popov (1977) and Kafanov & Popov (1977) considered

TABLE 1. Data matrix. "X" indicates polymorphism for states 0 and 1. "Y" indicates polymorphism for states 1 and 2. "Z" indicates polymorphism for states 1, 2 and 3.

Outgroup	1000011000	0432010000	0000100100	1011300000	00000001000
Plagiocardium	??????????	??????????	???????1?1	0111Z00000	00000001111
Maoricardium	1000011000	3032000000	00?0101001	1111300000	00000001111
Ciliatocardium	1000011100	22320X1000	0010101111	1110200000	00010001101
Profulvia	??????????	??????????	???????101	1110200?0	00010001101
Clinocardium	1010011100	32310X0010	0020100111	0000100010	10010001201
Fuscocardium	??????????	??????????	???????111	0001000?0	10010011201
Keenocardium	1010011100	22310X0010	00?0100101	0000000010	10000000201
Yagudinella	?????101??	??????????	???????211	0000100010	10010000201
Serripes	1011010100	2232001010	0010100201	0000000010	10000000201
Papillicardium	0000001001	3032000000	00?1100101	0010100000	00000000311
Parvicardium siculum	0000000001	4022000000	0??1100104	0000100000	00100000312
P. exiguum	0000011001	4012000000	0101100104	0010100000	00000000312
Cerastobyssum	0000000001	1032000000	01?1100104	0000100000	00000001311
Apiocardia	1000011101	2133000100	00?1100104	0010200000	00101112313
Trigoniocardia	0000011101	2113000100	00?1100104	0010100000	00001112313
Goniacardia	??????????	??????????	???????104	0010100000	00101112313
Lunulicardia	1000011001	4114110000	00?1100104	0010000000	01000012404
Corculum	0100000011	4114000100	0021100104	0010100000	01010000405
Fragum	0100011011	4112000100	00?1100004	0000300000	00000012303
Microfragum	01200XX011	2112100100	00?1100105	0010100000	00000001303
Ctenocardia	0100011011	2112000100	00?1100205	0010200000	00000001303
Americardia	0100011011	3112000100	00?1100105	0010000000	01000001303
Goethemia	10000000?0	3002000000	0200100102	0002100000	00000000311
Cerastoderma	1000000000	0322001001	0000100102	0000000000	00000001311
Hypanis	1000000000	5322001001	00?0100113	0000100000	0000???311
Didacna	1000000000	5322001001	00?0100113	0000100000	0000???311
Goniocardium	??????????	??????????	???????104	0012Y00001	00000000312
Avicularium	??????????	??????????	???????104	0002?10101	000????0?12
Byssocardium	??????????	??????????	???????104	0002?10102	000????0?12
Hippopus	?000100000	5320000001	10110101?4	0002?11202	000????0?12
Chametrachea	?000100000	5320000001	10112101?4	0002?11302	000????0?12
Tridacna	?001100000	5320000001	10112101?4	0002?11402	000????0?12
Persikima	?000100000	5320000001	10112101?4	0002?11502	000????0?12

Schedocardia as a genus ancestral to *Acanthocardia.* Keen (1969a, 1980) and Glibert & van de Poel (1970, 1973) also classified *Loxocardium* in the Cardiinae. Schneider (1993a, 1998) found that *Loxocardium* and *Orthocardium* were members of a monophyletic group with other Cenozoic cardiines.

Anatomical material of the type species of *Trigoniocardia, Cardium graniferum* Broderip & Sowerby, 1829, was unavailable, so *Trigoniocardia* is represented by *Cardium antillarum* Orbigny, in Ramon de la Sagra, 1842.

Sawkinsia, considered a tridacnid by Vokes (1953), Keen (1969a), and Jung (1976), was found to be a close relative of *Acanthocardia* and *Schedocardia* (Schneider, 1992, 1998). *Sawkinsia* aside, Stasek (1962), Rosewater (1965), and Keen (1969b) all agreed on the remaining genera and subgenera belonging to Tridacnidae. The type species of *Chametrachea* is *Tridacna crocea* Lamarck, 1819. *Tridachnes maxima* Röding, 1798, was selected to represent *Chametrachea* because of the availability of anatomical material.

Kafanov & Popov (1977) classified the Norian (Late Triassic) *Septocardia* as a tridacnid, and were followed by Scarlato & Starobogatov (1979). However, as Schneider (1992) pointed out, *Septocardia* does not have any of the apomorphies of tridacnines and may not even be a cardiid (Morris, 1978; Schneider, 1995).

There are over 90 named genera and subgenera of Lymnocardiinae, all but four of them extinct (Keen, 1969a; Bagdasarian, 1978; Vokes, 1980; Taktakishvili, 1987; Basch, 1990). Because specimens of the vast majority of these taxa, especially of the type species, are found only in eastern European museums, I did not attempt to undertake a detailed study of the phylogenetic relationships within the Lymnocardiinae. Lymnocardiines are represented by the Recent taxa *Cerasto-*

TABLE 2. Synapomorphies of interior nodes of tree number 15 (Fig. 34).

Node	Synapomorphies (character: state)
1	11:3, 12:0, 30:1, 31:0, 32:1, 34:4
2	49:1, 50:1, 51:1
3	16:0, 32:0, 34:0, 35:1
4	8:1, 11:2, 12:2, 23:1, 44:1, 50:0
5	17:1, 27:1, 31:1, 32:1, 35:2
6	3:1, 14:1, 19:1, 33:0, 39:1, 41:1, 49:2
7	11:3, 23:2, 29:1
8	35:0, 44:0, 48:0
9	4:1, 7:0, 14:2, 17:1, 28:2
10	6:0, 34:2, 48:0, 49:1
11	1:0, 10:1, 24:1, 34:3, 51:2
12	11:4, 22:1, 30:4
13	7:0
14	6:1, 13:1
15	11:2, 12:1, 18:1, 22:0, 23:2, 47:1, 48:2, 51:3
16	8:1, 14:3, 45:1, 46:1
17	1:1, 13:3, 43:1
18	2:1, 9:1, 50:0
19	11:4
20	14:4, 18:0, 42:1, 49:4, 51:4
21	30:5, 47:0, 48:1
22	35:2
23	7:0, 13:0, 30:2, 33:0
24	11:5, 12:3, 13:2, 20:1
25	17:1, 34:0, 48:1
26	29:1, 30:3
27	5:1, 14:0, 21:1, 23:1, 24:1, 25:0, 26:1, 30:4, 41:1, 51:2
28	36:1, 38:1
29	40:2
30	37:1, 38:2
31	25:2, 38:3
32	38:4

derma, *Hypanis* (*Monodacna*), and *Didacna*. Anatomical material of the type species of *Hypanis* (*Monodacna*), *Corbula caspia* Eichwald, 1829, was unavailable, so *H.* (*Monodacna*) is represented by *Glycimeris colorata* Eichwald, 1829.

Nordsieck (1969) erected the subfamily Cerastodermatiinae for *Cerastoderma* and *Parvicardium*. Two monotypic taxa subsequently named (*Cerastobyssum* Petersen & Russell, 1973, and *Goethemia* Lambiotte, 1979) were included in Cerastodermatiinae by Voskuil & Onverwagt (1989), who also included *Papillicardium* in Cerastodermatiinae (as a subgenus of *Parvicardium*). Nordsieck had included *Papillicardium* in Fraginae. Although each are monotypic, the relationships of *Goethemia* and *Cerastobyssum* are uncertain, and these taxa are included in the analysis. The type species of *Parvicardium* is also uncertain. Two species of *Parvicardium* are therefore included: (1) *Cardium siculum* Sowerby, 1841, which Voskuil & Onverwagt (1989) consider to be its type species; and (2) *Cardium exiguum* (Gmelin, 1791), the type species according to most other authors.

Afrocardium was erected by Tomlin (1931) as a subgenus of *Fragum*. Keen (1951, 1969a, 1980) classified *Afrocardium* as a subgenus of the fragine *Ctenocardia;* Popov (1977) synonymized *Afrocardium* with *Plagiocardium*. All eight species that Tomlin placed in *Afrocardium* are rare, have been only superficially described, are unknown anatomically, and have received virtually no attention since Tomlin (1931). Specimens were not available during the preparation of my preliminary analysis (Schneider, 1992). Subsequently, I have been able to examine the shells of several species of *Afrocardium,* including type and non-type specimens of the type species, *A. shepstonense* (Tomlin, 1931), and to dissect a specimen of *A. exochum* (Melvill, in Melvill & Standen, 1906). These species bear none of the apomorphies of Fraginae and several apomorphies of Cardiinae. Some authors (Habe, 1951; Kira, 1955, 1962; Cotton, 1961; Kuroda et al., 1971; Oyama, 1973; Fischer-Piette, 1977; Wilson & Stevenson, 1977) have included the species *Cardium ebaranum* Yokoyama, 1927 (Pleistocene to Recent), and *Cardium erugatum* Tate, 1889 (Recent), in *Afrocardium*. After examination of the shells of these species, and of the anatomy of *C. erugatum,* it was determined that they belonged in *Microfragum* (with the Pleistocene specimens of *C. erugatum* being the only known fossils attributable to *Microfragum*). *Afrocardium*, a member of the Cardiinae and not the Fraginae, is not included in the present analysis.

Selection of Outgroup

Selection of outgroup was based on the results of two previous studies. In the preliminary study (Schneider, 1992), the subfamily Cardiinae was shown to be the sister taxon to Clinocardiinae + Fraginae + Tridacninae + Lymnocardiinae. Among the least derived cardiines was *Acanthocardia*. In a phylogeny of Cretaceous to Eocene cardiids (Schneider, 1993a, 1998), the Eocene fragines and tridacnines formed a monophyletic group, with *Schedocardia* + *Sawkinsia* as its sister taxon. *Sawkinsia* is known only from molds and recrystallized specimens (Cox, 1941; Jung, 1976; Kojumdgieva & de la Torre, 1982; pers.

obs.). The morphology of many characters is still unknown, including ornamental microstructure and many hinge characters (Schneider, 1992, 1993a, 1998). *Sawkinsia* is therefore not considered in the outgroup. As stated previously, *Schedocardia* is considered closely related to *Acanthocardia* (Keen, 1951, 1969a, 1980; Kafanov & Popov, 1977; Popov, 1977). Therefore, the outgroup for the present analysis is an ancestor with conchological states taken from *Schedocardia* and anatomical states taken from *Acanthocardia*. The analysis also was run with both *Acanthocardia* and *Schedocardia* as outgroups, with the same phylogenetic results as those presented here.

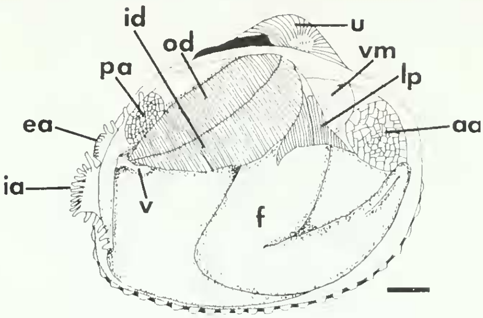

FIG. 1. Anatomy of *Clinocardium nuttallii* (live specimen, Monterey Bay; Schneider, 1994). Right valve and mantle removed. Scale bar = 5 mm.

DESCRIPTION OF CHARACTERS

I. Anatomical characters

External views (shell removed) of three taxa of cardiids is presented in Figures 1 and 2.

A. Labial palps

1. Size of labial palps (Figs. 3, 4). States: (0) small—less than one-fifth length of animal, (1) large—greater than one-fifth length of animal.

(Tridacnines are scored missing for this character. See Discussion)

2. Labial palp tips (Figs. 3, 4): (0) pointed, (1) blunt.

3. Insertion of labial palps and inner demibranch into oral groove (og; Figs. 3, 4): (0) inner demibranch inserted between labial palps, (1) inner labial palp (ip) connected to bottom of inner demibranch (id), (2) inner demibranch inserted behind inner labial palp

B. Ctenidia

4. Food groove on outer demibranch (od; Fig. 5). An outer food groove on *Serripes groenlandicus* (Mohr, 1786) is reported here for the first time. Stasek (1962) reported that *S. groenlandicus* lacked a food groove on its outer demibranch, but this structure was present on every specimen of *S. groenlandicus* that I examined. Yonge (1936) reported that *Tridacna* (*Persikima*) *derasa* (Röding, 1798) was the only giant clam with a food groove on its outer demibranch. Stasek (1962) reported that *Hippopus hippopus* (Linné, 1758) and *T. derasa* had food grooves on their outer demibranchs. Rosewater (1965) stated that a food groove on the outer demibranch was present in *Tridacna* (*Tridacna*) *gigas* (Linné, 1758) and *H. hippopus* but absent in *T. derasa* and all other giant clams. Lucas et al. (1991) report that *T. gigas* is the only giant clam with a food groove on its outer demibranch, and my anatomical studies confirm the observations of Lucas et al. States: (0) absent, (1) present.

5. Ctenidial filaments. Tridacnines have more than 60 filaments per ctenidial plica. Other cardiids have less than 30 filaments per plica (Ridewood, 1903). States: (0) few (< 30), (1) numerous (> 60).

C. Foot

6. Lateral ridges on foot (lr; Fig. 6): (0) absent, (1) present.

7. Ventral ridge on foot (vr; Fig. 6): (0) absent, (1) present.

8. Ventral papillae (vp; Figs. 6, 7). Gould (1841) named *Serripes* for "the serrated margin of the foot" of *Cardium groenlandicum* Mohr, 1786. Kafanov (1980) described ventral papillae on either side of the byssal groove on all Recent clinocardiines, and I discerned ventral papillae on either side of the byssal groove of the fragines *Trigoniocardia* and *Apiocardia*. States: (0) absent, (1) present.

D. Siphons and tentacles

9. Valvule (v; Figs. 1, 2). A semicircular flap of tissue on the interior of the siphonal apparatus, just dorsal to the incurrent aperture, was called the languette or curtain valve by Dall (1889). Pelseneer (1911) and Schneider (1992, 1994) termed this structure the valvule. Pelseneer (1911) first noted that some fragines have larger valvules. States: (0) small or absent, (1) large.

10. Perisiphonal suture (pss; mispelled as periphonal suture in Schneider [1992]; Fig. 8). The perisiphonal suture is the tissue separating the incurrent aperture from the pedal gape

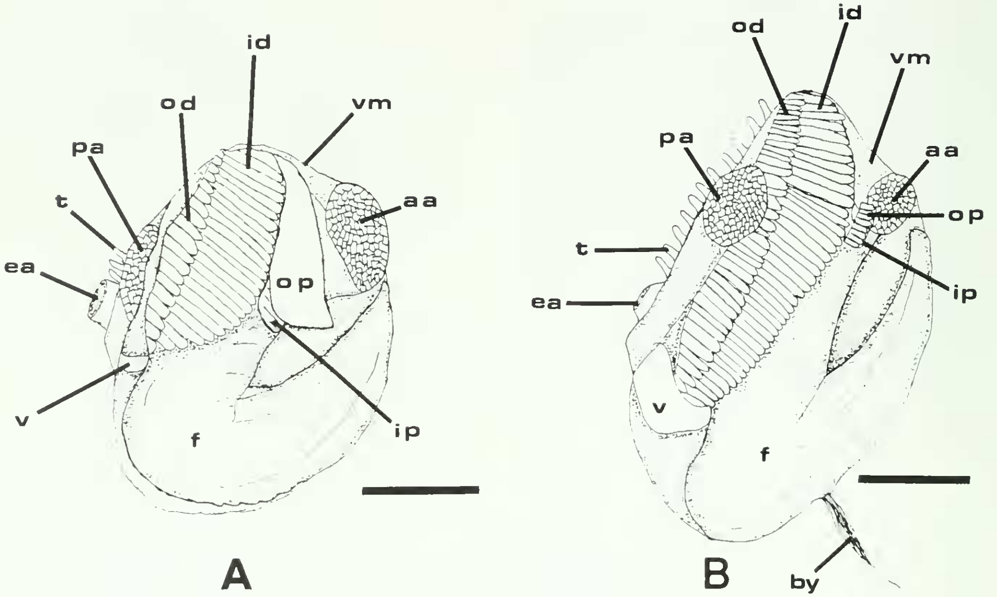

FIG. 2. Anatomy of (A) *Trigoniocardia* (*Apiocardia*) *obovale* (ANSP 316937) and (B) *Fragum fragum* (ANSP 289145). Shell and right mantle removed in both specimens. A, scale bar = 4 mm; B, scale bar = 5 mm.

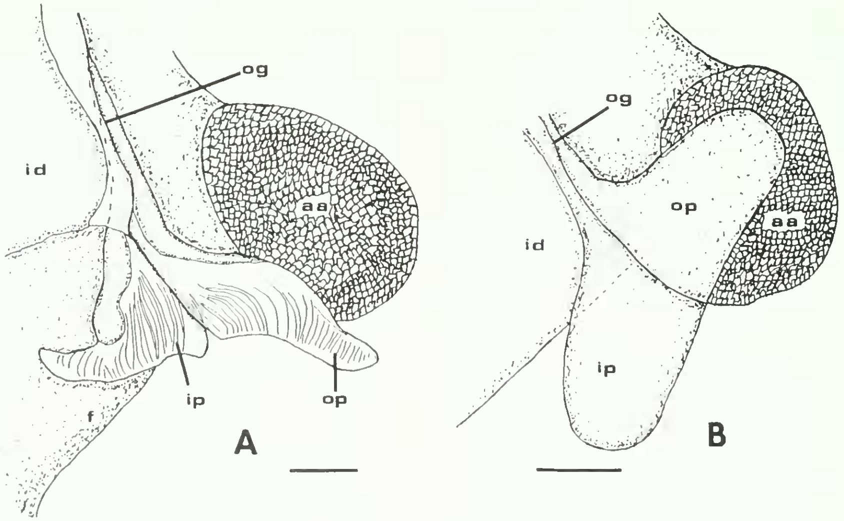

FIG. 3. Labial palps (right). A, *Ciliatocardium ciliatum* (USNM 604850). Dotted line indicates location of dorsal extension of inner palp behind inner demibranch. Scale bar = 5 mm. B, *Microfragum festivum* (AM C.164061). Dotted line indicates location of inner demibranch behind labial palps. Scale bar = 1 mm.

(pg). All fragines and only fragines lack a perisiphonal suture. Dall (1895) and Pelseneer (1911) have previously noted this anatomical structure. States: (0) present, (1) absent.

11. Location of dorsalmost tentacles around siphonal area (Fig. 8): (0) at bottom of posterior adductor muscles, (1) one-quarter up adductors, (2) half-way up adductors, (3) top of adductors, (4) beyond top of adductors, (5) around siphonal apertures only.

12. Tentacle pattern (Fig. 8): (0) numerous

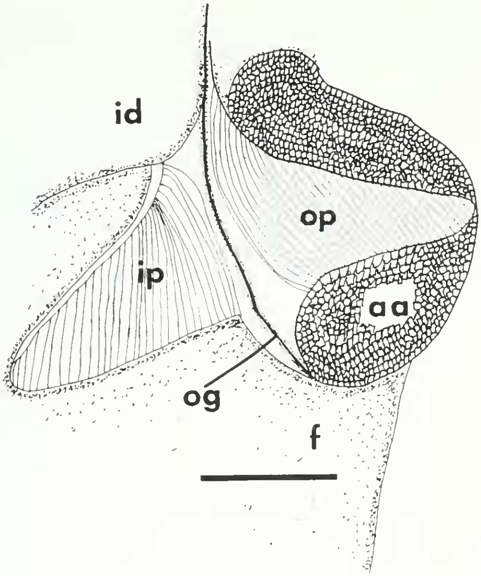

FIG. 4. Labial palps (right) of *Clinocardium nuttallii* (Schneider, 1994). Scale bar = 5 mm.

tentacles on both periphery and central portion of intersiphonal area, (1) numerous tentacles on periphery of intersiphonal area, few or no tentacles on central portion of intersiphonal area, except around siphonal apertures, (2) tentacles few, but located both on periphery and central portion of intersiphonal area, (3) on siphons only, (4) numerous tentacles around siphons, few tentacles elsewhere.

E. Intestine

13. Path of intestine (Figs. 9, 10). *Cerastoderma, Hypanis, Didacna, Parvicardium siculum,* and tridacnines have intestines that may be of either three or four loops. (Johnstone [1899] discusses the intestine of *Cerastoderma edule*.) Complex intestines are those that typically have eleven loops. Two taxa with somewhat less complicated intestines, *Apiocardia* (Fig. 10A) and *Serripes* (Fig. 10D), are also coded for this character state, for the general *pathway* of the intestine in *Apiocardia* and *Serripes* is similar to the eleven-looped form. When the data set is run with the states for *Apiocardia* and *Serripes* coded as autapomorphies, the results are the same as the results presented here, except that the most parsimonious trees are each two steps longer. The intestine of *Goethemia* has no loops. Most fragines have guts with a single loop. States: (0) no loops, (1) one loop, (2) 3 to 4 loops, (3) > 4 loops.

F. Stomach (Fig. 11).

Yonge (1936) and Purchon (1955) described and illustrated the stomach of several species of giant clams. Purchon (1960a) based his description of the cardiid stomach on Graham's (1949) description and figure of *Cerastoderma edule*. Nakazima (1964a, b) described and illustrated the stomachs of *Hippopus hippopus, Tridacna* (*Chametrachea*) *maxima* (Röding, 1798) (= *Tridacna elongata*), and *Nemocardium bechei* (Reeve, 1847). Starobogatov (in Kafanov & Popov, 1977) described, but did not illustrate, the stomachs of species belonging to twelve genera of cardiids. The species that Starobogatov examined were not stated. It is therefore important to emphasize that discrepencies between my data and those of Starobogatov's may be due to species-level differences. (Schneider, 1992, discusses use of *Cerastoderma edule* to represent *Cerastoderma* versus Starobogatov's use of *Cerastoderma glaucum* [Bruguière, 1789].) Kafanov & Popov's use of sorting areas of the stomach as key characters in bivalve phylogeny was discussed by Schneider (1992; see Purchon, 1960a: 481). Purchon (1987a) reviewed the literature on cardiid stomach anatomy. Schneider (1994) described and illustrated the stomachs of *Nemocardium* (*Keenaea*) *centifilosum* (Carpenter, 1864) and *Clinocardium nuttallii*. The terminology of stomach sorting areas is after Purchon (1960a).

14. Major typhlosole (T1) path. Purchon (1960a) put the Cardiidae and Tridacnidae into his type V stomach group. The diagnostic feature of type V bivalve stomachs is the extension of the major typhlosole and intestinal groove into two caeca (left and right). In bivalves with type V stomachs, the major typhlosole exists the combined midgut/style sac (ss), anteriorly traverses the stomach floor, and enters the right caecum (rc). The major typhlosole then emerges from the right caecum, traverses laterally across the anterior of the stomach floor, and enters the left caecum (lc). Within the left caecum, the major typhlosole may terminate in a spiral (as in tridacnines; sf). All published accounts of cardiid stomachs are consistent with this description. This is the pathway of the major typhlosole in most of the cardiids in the present analysis. However, Schneider (1994) found the major typhlosole

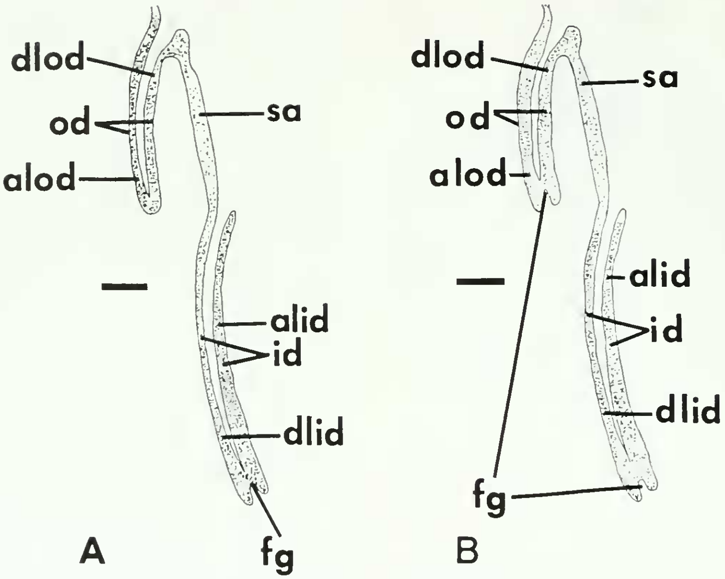

FIG. 5. Cross-section through ctenidia, showing food grooves. A, *Clinocardium nuttallii* (from Schneider, 1994). B, *Serripes groenlandicus* (USNM 600836). Scale bars = 5 mm.

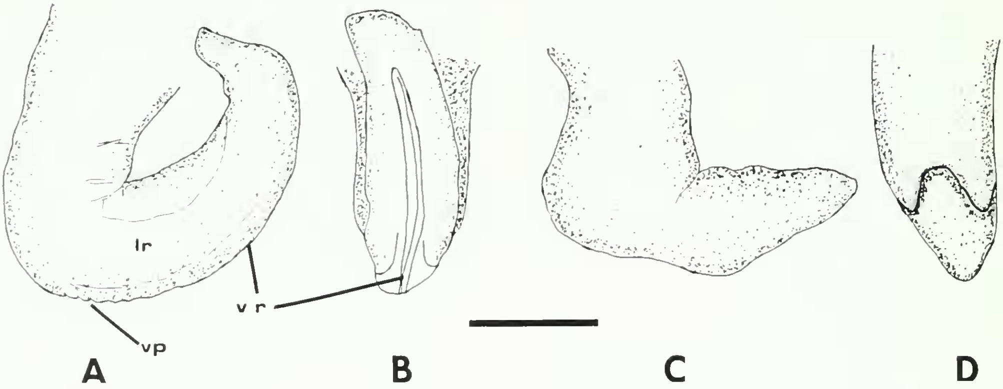

FIG. 6. Feet. A, lateral, and B, anterior view of foot of *Apiocardia obovale* (ANSP 316937). Scale bar = 4 mm. C, lateral, and D, anterior view of foot of *Cerastoderma edule*, specimen dissected live. Scale bar = 2 mm.

in *Clinocardium nuttallii* split in two, giving rise to left and right branches that separately enter the left and right caeca, respectively. In bivalves with stomach type IV of Purchon (1958, 1960a), the major typhlosole emerges from the midgut, traverses forward across the stomach floor and then curves to the left. Finally, the major typhlosole terminates within or close to the entrance of the left caecum. Purchon (1960a, b) considered the bivalve groups of stomach types I, II, III, and V to be monophyletic groups. However, Purchon (1960a, b) proposed that many bivalves with type IV stomachs — Sphaeridae, Lucinidae, Thyasiridae, Donacidae, *Chama multisquamosa* [Reeve, 1846] — were progenetically derived from bivalves with type V stomachs. Most of these forms are smaller in size than their closest relatives, the latter forms having type V stomachs. Purchon (1960a, b) therefore was of the opinion that the reversion to a type IV stomach in these bivalves is related to miniaturization. Purchon (1987a) distinguished these bivalves which secondarily evolved a

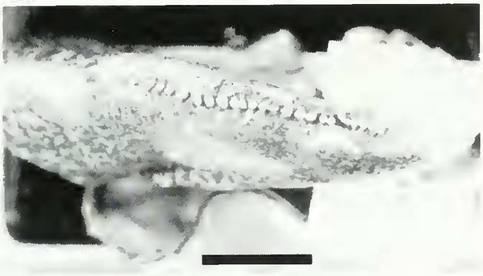

FIG. 7. Ventral view of foot of *Serripes groenlandicus* (USNM 600836), with prominent ventral papillae. Scale bar = 40 mm.

type IV stomach by erecting a new group for them, stomach type IVB. Purchon (1987a) considered only *C. multisquamosa,* the donacids, and the tellinids with type IVB stomachs to have evolved progenetically. Purchon (1987a) termed the stomachs of lucinids, thyasirids, and the pisidiid *Sphaerium corneum* (Linné, 1758) "secondarily simplified."

In the stomachs of *Trigoniocardia antillarum* and *Apiocardia obovale* (Sowerby, in Broderip & Sowerby, 1833) (Figs. 15J, K), the major typhlosole is as in type IV bivalve stomachs. The major typhlosole emerges from the combined midgut/style sac, traverses anteriorly across the stomach floor and then enters the left caecum, where it terminates. In *Lunulicardia retusa* (Linné, 1767) (Fig. 15L) and *Corculum cardissa* (Linné, 1758), the major typhlosole exits the midgut/style sac, and then

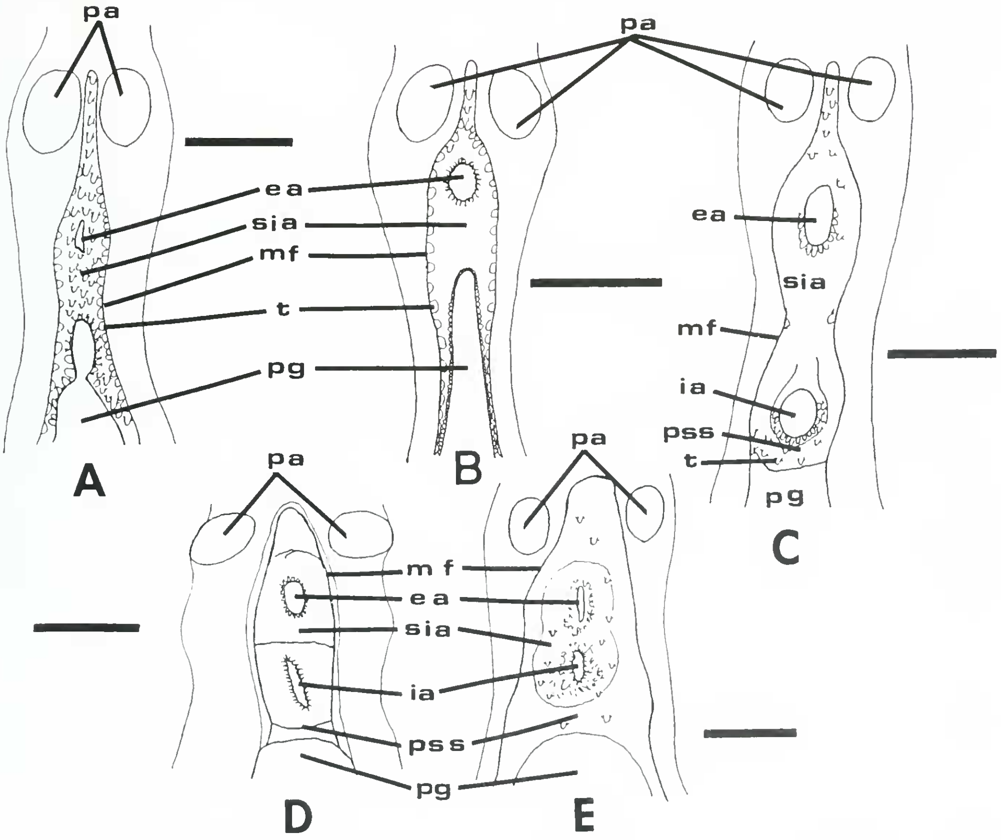

FIG. 8. Tentacles and siphons. A, *Papillicardium papillosum* (MNHN, unnumbered). Scale bar = 2 mm. B, *Ctenocardia symbolica* (ANSP 229873). Scale bar = 3 mm. C, *Serripes groenlandicus* (USNM 600836). Scale bar = 4 mm. D, *Hypanis* (*Monodacna*) *colorata* (USNM 769939). Scale bar = 2 mm. E, *Acanthocardia aculeata* (NHM Acc.2322). Scale bar = 10 mm.

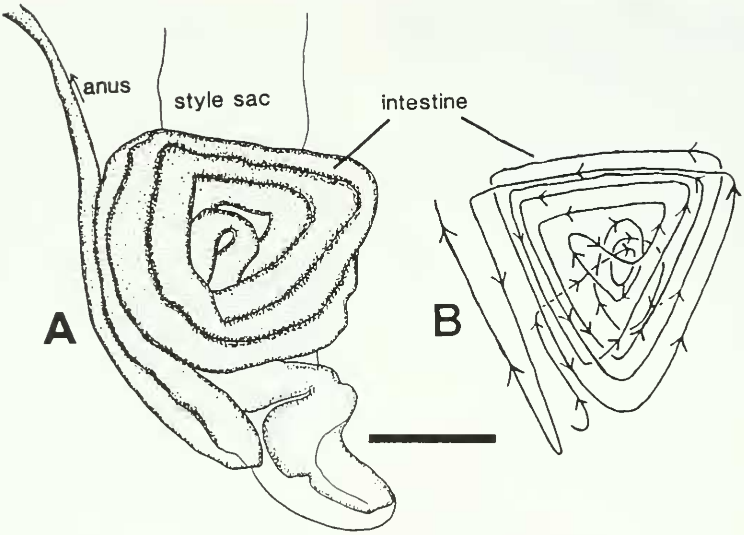

FIG. 9. Camera lucida drawing of intestine (A) of *Clinocardium nuttallii*, as seen from right side, and (B) diagram depicting pathway of intestine from exit of style sac/midgut to exit from visceral mass. Scale bar = 2 mm. From Schneider, 1994.

traverses anteriorly until it enters the right caecum, where it terminates. States: (0) T1 to RC, then LC, then spirals, (1) splits: T1r to RC, T1l to LC, (2) T1 to RC then LC, (3) T1 to LC, (4) T1 to RC.

15. Location of right caecum: (0) right side, (1) central.

16. Relative position of caeca. Starobogatov, in Kafanov & Popov, 1977, considered the relative position of the gastric caeca in erecting the five different cardiid stomach types. The caeca are "parallel" (i.e., a line connecting the midpoints of the caeca is perpendicular to a line from the esophagus to the style sac/midgut) in Cardiinae and Clinocardiinae, and not parallel in Lymnnocardiinae, Fraginae, and Protocardiinae (all subfamilies *sensu* Kafanov & Popov). From my dissections, I have found that the caeca are parallel in all ingroup taxa, except for *Lunulicardia retusa* (Fig. 11L, M). This character state is polymorphic for clinocardiines except for *Serripes groenlandicus* (Fig. 11E, F); caeca may be parallel or the right caecum may be more anterior. The caeca are not parallel in the cardiine *Acanthocardia aculeata* (Linné, 1767) (Fig. 11A), from which I have taken the anatomical data for the outgroup. States: (0) caeca parallel, (1) right caecum anterior to left caecum.

17. Tertiary typhlosole (T3). A typhlosole-like structure, just ventral of the posterior sorting area (SA3), is present in lymnocardiines and the clinocardiines *Ciliatocardium ciliatum* (Fabricius, 1780) (Fig. 11C, D) and *Serripes groenlandicus* (Fig. 11E, F). This structure is prominent in Graham's (1949) figure of the stomach of *Cerastoderma edule,* but is unlabeled and is not mentioned in the text. This structure is not mentioned in Kafanov & Popov (1977). States: (0) absent, (1) present.

18. Location of style sac: (0) posterior, (1) anterior.

19. Raised bar (rb). Some clinocardiines have a raised structure across the middle of the stomach floor. In *S. groenlandicus* (Fig. 11E, F), the raised bar is anterior to the caeca. In other clinocardiines, the raised bar is posterior of the caeca. States: (0) absent, (1) present.

20. Ridge (r). Graham (1949) discussed a ridge that runs transversely and obliquely across the anterior stomach floor, below the esophagus. This structure (labeled RCE by Graham) is found in lymnocardiines and tridacnines. States: (0) absent, (1) present.

21. Esophageal sorting area (SA7 or SAE). The esophageal sorting area is present in all cardiids except tridacnines. This has been noted by Purchon (1987a). States: (0) present, (1) absent.

G. Reproductive characters.

Data for characters 22 and 23 from Lovén (1848), Lacaze-Duthiers (1854), Grobben

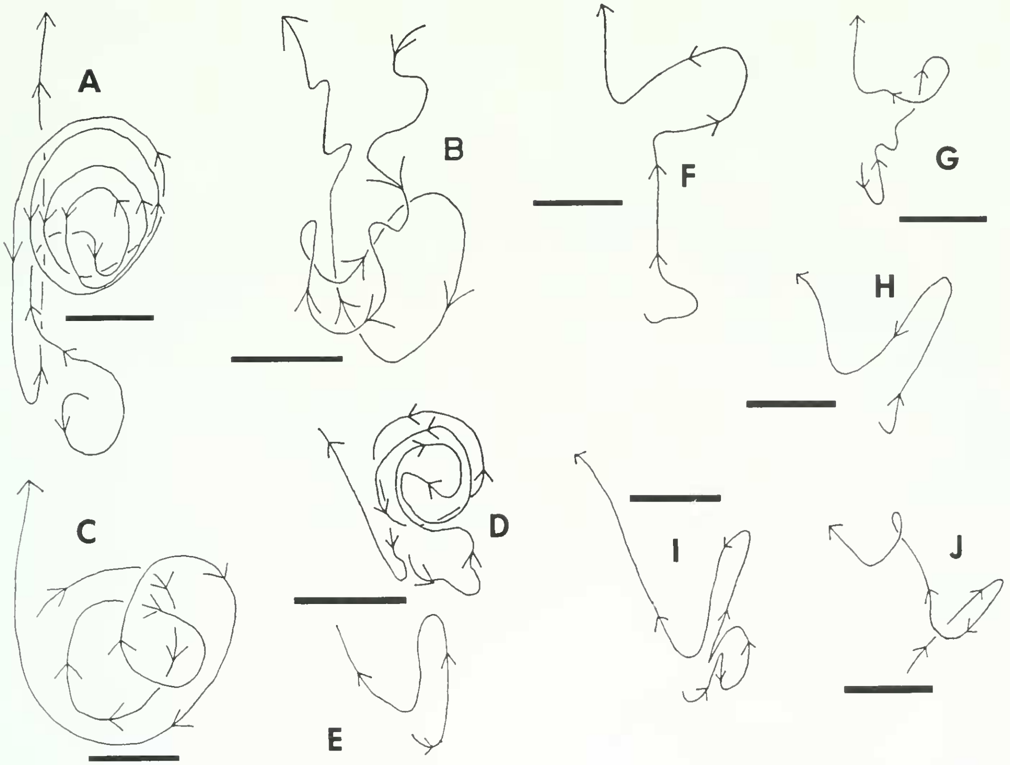

FIG. 10. Intestinal pathways. A, *Serripes groenlandicus* (USNM 600836). B, *Tridacna* (*Chametrachea*) *maxima* (ANSP A3276). C, *Parvicardium siculum* (AMNH 226511). D, *Apiocardia obovale* (ANSP 316937). E, *Trigoniocardia antillarum* (USNM 857540). F, *Lunulicardia retusa* (ANSP 302424). G, *Fragum fragum* (ANSP 289145). H, *Microfragum festivum* (AM C.164061). I, *Americardia media* (ANSP 297243). J, *Ctenocardia symbolica* (ANSP 229873). All scale bars = 2 mm, except for B (10 mm) and G (4 mm).

(1898), Johnstone (1899), Pelseneer (1911), Edmondson (1919), Stephenson (1934), Thorson (1936), Yonge (1936, 1981), Wada (1952, 1954), Matveeva (1953), Ockelmann (1959), Petersen (1958), LaBarbera (1975), Jameson (1976), Gwyther & Munro (1981), Gallucci & Gallucci (1982), Alcazar & Solis (1985), Braley (1985), Dolgov (1991) and Fitt (1991).

22. Larvae. In *Parvicardium exiguum* and *Cerastobyssum*, the eggs are attached singly to the bottom by means of a double mucous membrane (Lovén, 1848), similar to that of some species of *Macoma* and *Astarte* (Thorson, 1936). Presumably, these eggs are subsequently fertilized by sperm emitted into the water column. In *Goethemia*, fertilized larvae are brooded in pouches formed by folds of the ventral part of the mantle, and the young hatch when the shell length reaches about 1.2 mm (Matveeva, 1953; Fig. 12). In all other cardiids, both sperm and egg are emitted into the water column where fertilization takes place (Pelseneer 1911; Yonge, 1936). States: (0) fertilization in water column, (1) egg capsules, (2) brooded.

23. Sex: (0) dioecious: separate sexes throughout entire life history, (1) protandric: male stage preceeds female stage in life history, (2) monoecious: hermaphroditic through entire life history.

H. Other anatomical characters

24. Byssus (by; Figs. 2B, 13). Larval and early juvenile stage cardiids have a functional byssal gland (Pelseneer, 1911; Yonge, 1936). A functional byssal gland is present in the adults of fragines and *Chametrachea*. Other tridacnines have a functional byssal gland in older juveniles or sub-adults, until they are large enough to be held in place by their own weight. The loss of a functional byssus in

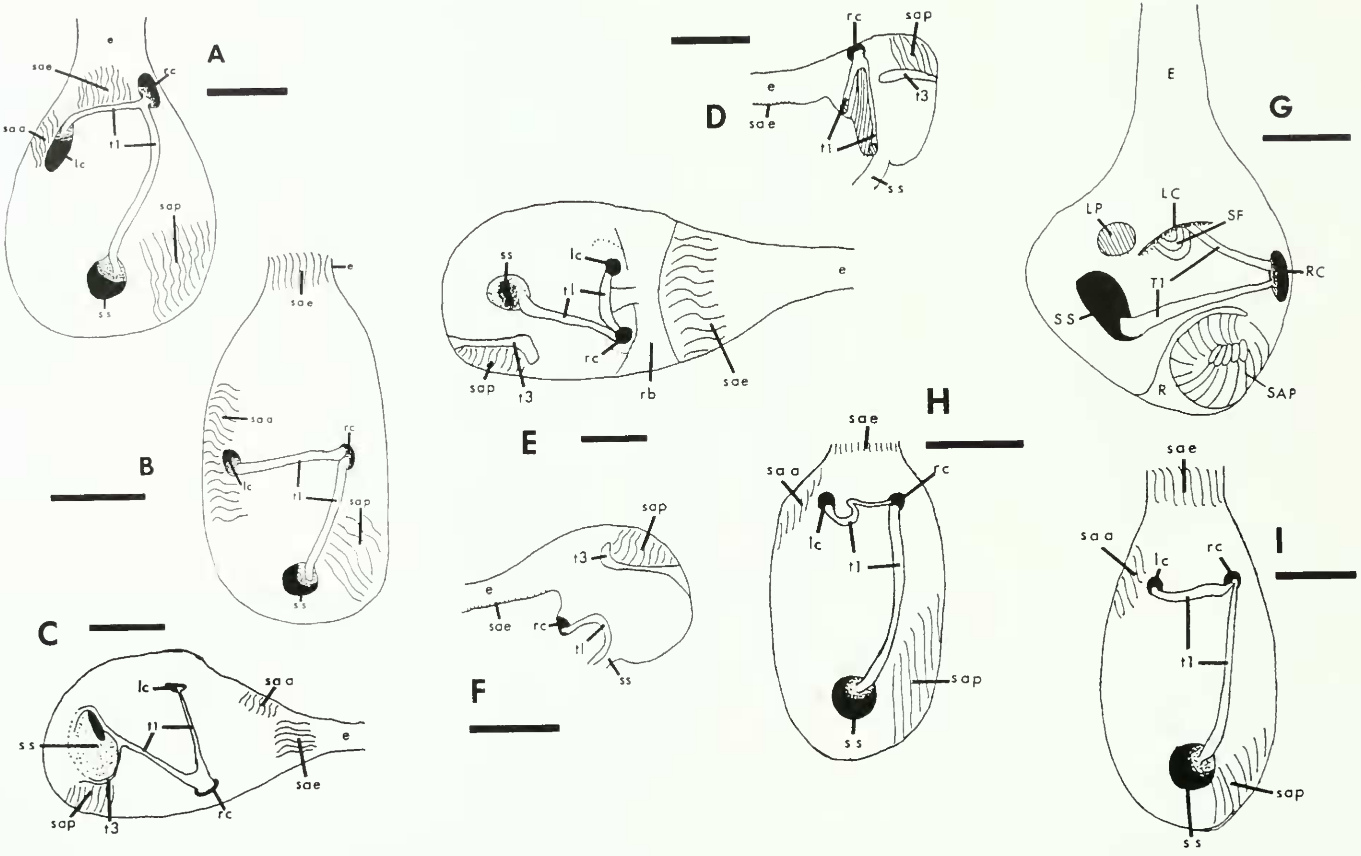

FIG. 11. Stomach morphology. All views of stomach are viewed from top of stomach looking downward. Stomach cut open at top along anterior-posterior axis. View distorted as in Purchon (1955, 1958, 1960a, 1987a) and Nakazima (1964a, b) so that structures on side and top of stomach appear to be on stomach floor in these two-dimensional drawings. Notably capacious stomachs are illustrated with additional views. The anterior sorting area (saa, or SA8) of *Serripes groenlandicus* is present, on the interior of the top of the stomach. A, *Acanthocardia aculeata* (NHM Acc.2322). Scale bar = 3 mm. B, *Maoricardium pseudolatum* (AM C.164058). Scale bar = 6 mm. C, D, *Ciliatocardium ciliatum* (USNM 604850). C, stomach floor as seen from top, scale bar = 2 mm; D, right side of stomach, scale bar = 4 mm. E, F, *Serripes groenlandicus* (USNM 600836). E, stomach floor as seen from top, scale bar = 2 mm; F, right side of stomach, scale bar = 5mm. G, *Tridacna* (*Chametrachea*) *maxima* (ANSP A3276). Scale bar = 2 mm. H, *Parvicardium siculum* (AMNH 226511). Scale bar = 1 mm. I, *Papillicardium papillosum* (MNHN, unnumbered). Scale bar = 1 mm.

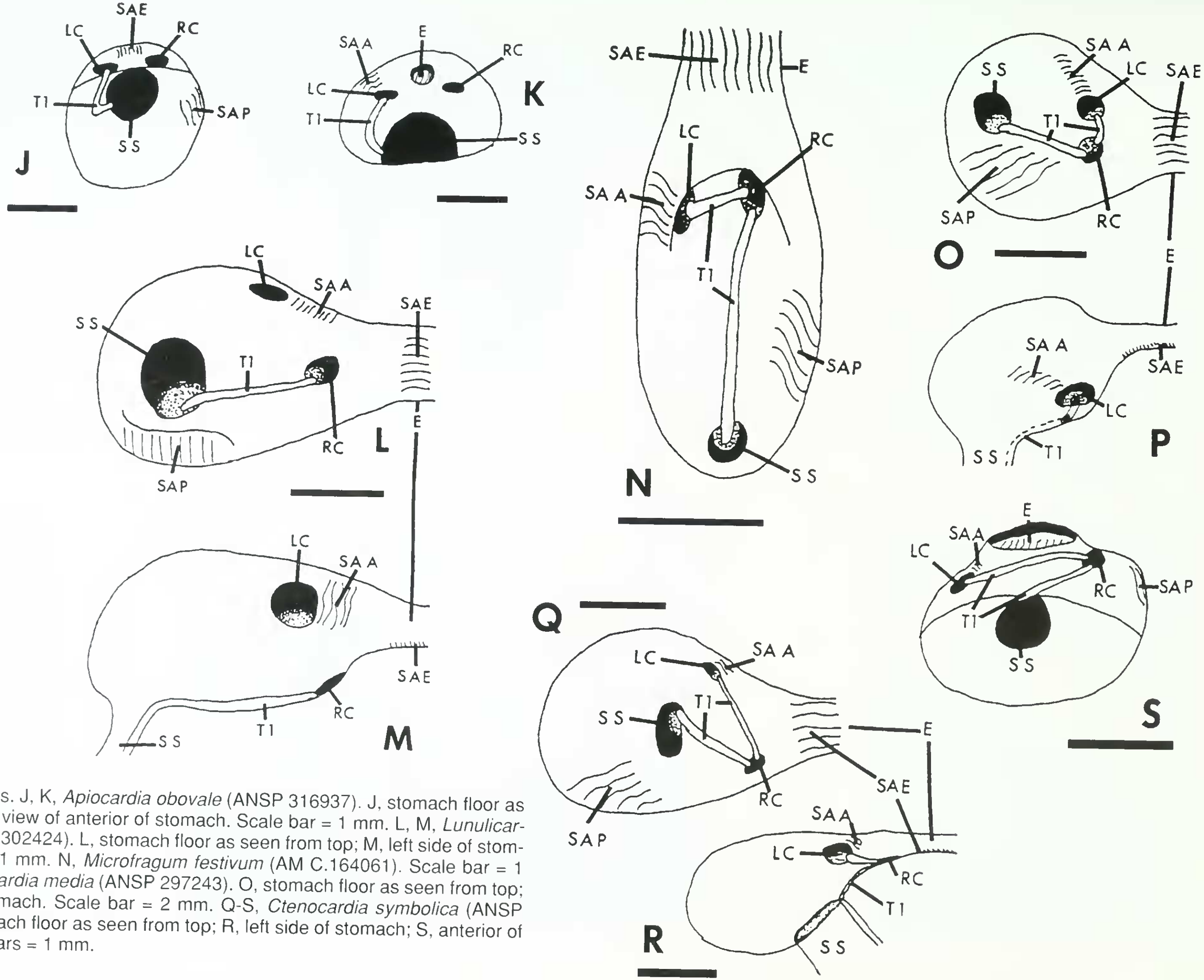

FIG. 11. Continues. J, K, *Apiocardia obovale* (ANSP 316937). J, stomach floor as seen from top; K, view of anterior of stomach. Scale bar = 1 mm. L, M, *Lunulicardia retusa* (ANSP 302424). L, stomach floor as seen from top; M, left side of stomach. Scale bar = 1 mm. N, *Microfragum festivum* (AM C.164061). Scale bar = 1 mm. O, P, *Americardia media* (ANSP 297243). O, stomach floor as seen from top; P, left side of stomach. Scale bar = 2 mm. Q-S, *Ctenocardia symbolica* (ANSP 229873). Q, stomach floor as seen from top; R, left side of stomach; S, anterior of stomach. Scale bars = 1 mm.

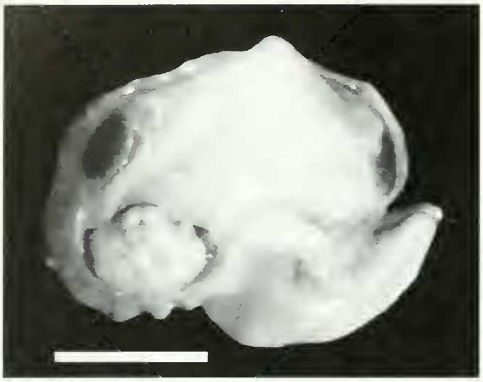

FIG. 12. *Goethemia elegantula* (SMNH 883) as seen from right side. Note brood pouch. Scale bar = 2 mm.

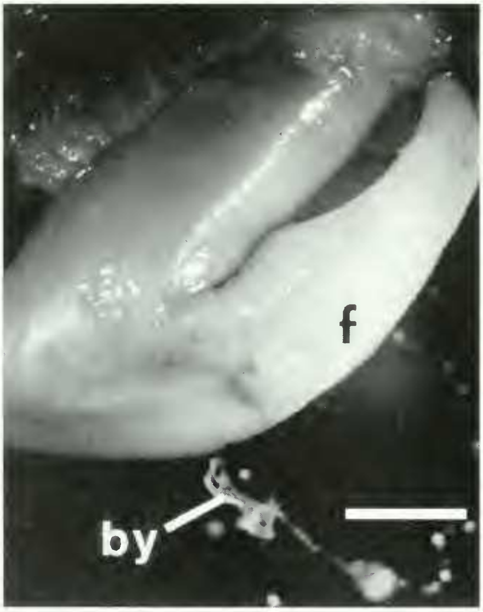

FIG. 13. Foot and byssal threads of *Fragum fragum* (ANSP 237102). Scale bar = 4 mm.

these forms is considered a secondary modification of a functional adult byssus (see Discussion). Petersen (1958), Yonge (1962), Petersen & Russell (1971), Lambiotte (1979), Yankson (1986), and Voskuil & Onverwagt (1989) discuss *Cerastoderma, Papillicardium, Parvicardium,* and *Cerastobyssum.* Pelseneer (1911) covers *Lunulicardia* and *Corculum,* and Kawaguti (1950), Savazzi (1985), and Severin & Cooper (1989) discuss *Corculum.* Rosewater (1965) and Yonge (1936, 1981) cover the tridacnines. States: (0) present in larval and early juvenile stage only, (1) present in later ontogeny, may be lost as adults.

25. Eyes. Most cardiids have simple, inverse eyes (Johnstone, 1899; Zugmayer, 1904; Weber, 1908; Pelseneer, 1911; Roche, 1925; Barber & Land, 1967; Barber & Wright, 1969). Tridacnines, except for *Hippopus* and *Tridacna* (*Persikima*) *tevoroa* Lucas et al., 1990, have hyaline organs (Yonge, 1936, 1981; Stasek, 1966; Kawaguti & Mabuchi, 1969; Fankboner, 1980; Wilkens, 1984, 1988, Lucas et al., 1991). *Hippopus* and *T. tevoroa* have neither simple inverse eyes nor hyaline organs. States: (0) absent, (1) simple inverse, (2) hyaline organs.

26. Mantle margins. The ventral, inner mantle folds of tridacnines are much larger than in other cardiids (Yonge, 1982; Morton, 1988). States: (0) small, (1) large.

B. Periostracum

27. Periostracal cilia (Fig. 14): (0) absent, (1) present.

C. Conchological characters

A. Shell exterior

28. Posterior margin. Discussed by Schneider (1995). (0) digitate, (1) crenulate, (2) smooth.

29. Beak gyry (Fig. 15). Most cardiids have slightly prosogyrous beaks or umbos (Wilson & Stevenson, 1977). Keen (1936) named *Clinocardium* for its strongly prosogyrous beaks. States: (0) weakly prosogyrous, (1) strongly prosogyrous. This character is coded as missing for the Recent tridacnines (see Discussion).

30. Shell shape (Fig. 16). Cardiids, like most bivalves, change the shape of their shell during ontogeny. Because of accretionary growth of bivalve shells, the shape at time 1 depends on the shape of the shell at time 0. This is a causal sequence and can be ordered under Alberch's (1985) criterion. Therefore, a character state tree can be constructed for shell shape. Although there have been several attempts to describe the ontogeny of bivalve shell shape (Raup, 1966; Lovtrup & Lovtrup, 1988; Checa, 1991; Johnston et al., 1991; Ackerly, 1992a, b), a rigorous method of converting morphometric information on bivalve ontogeny into cladistic character states

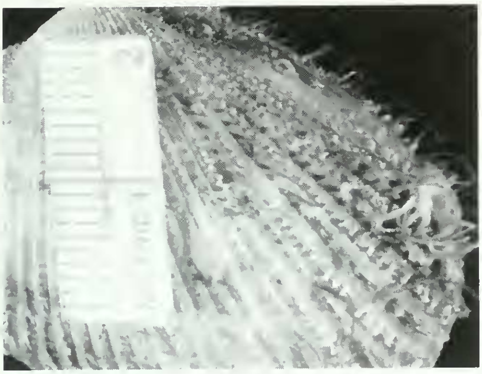

FIG. 14. Periostracal cilia of *Maoricardium pseudolatum* (AM C.164058). Scale indicated in figure.

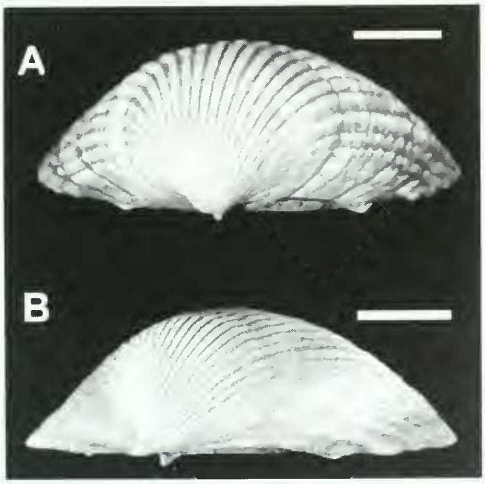

FIG. 15. Beak gyry. A, *Cerastoderma edule*, right valve (FMNH 278010), scale bar = 10 mm. B, *Clinocardium nuttallii*, right valve (FMNH 278016), scale bar = 20 mm.

has yet to be devised. In this study, the shell shapes exhibited by cardiids have been placed in six states, each of which can be described semi-quantitatively. Most cardiids go through at least two of the shell shape character states during ontogeny (hence the ability to construct character state trees; Table 3). *Maoricardium*'s and *Profulvia*'s shell shapes are terminal autapomorphies and are coded for the last ontogenetic state which fits on the character state tree. I follow the method proposed by Mabee & Humphries (1993) and consider the entire ontogenetic sequence as a single character state rather than coding the condition at each ontogenetic stage as a separate character. See Discussion for the coding of *Byssocardium, Hippopus, Chametrachea, Tridacna,* and *Persikima*. Shell shape can be determined by using the following key (Schneider, 1998, defines and illustrates the terms.) Schediform shell shape and oval shell shape are both preceded in ontogeny by circular shell shape (Schneider, 1998). The conchological component of the outgroup, *Schedocardia,* has a schediform shell shape. Therefore, schediform shell shape is considered the more basal state on the basis of outgroup comparison, not ontogeny. It should be noted that the "quadrate-short" shell shape of some fragines is not homologous to the "quadrate-short" shell shape of various taxa considered in Schneider (1995, 1998), because the ontogenetic pathway is vastly different.

Shell Shape Character Key

1. Apparent height (AH) > height (H) 2
   AH = H 3
2. Carina strong . . . . trigonal
   (includes "triangular" of Schneider, 1998)
   Carina weak or absent . . . . oval
3. H/length (L) > 1.0 . . . . . . .quadrate-short
   1.0 > H/L > 0.9 4
   H/L < 0.9 . . . . hypaniform
4. Post-hinge length (PHL) < (0.2) × L
   . . . . schediform
   PHL > (0.2) × L . . . . cerastiform

States: (0) schediform, (1) oval, (2) cerastiform, (3) hypaniform, (4) trigonal, (5) quadrate-short.

Character state tree:

```
0– –1– –4– –5
    |
    |
    2– –3
```

Schneider (1998) discusses the next three characters.

31. Primary raised thread: (0) absent, (1) present.

32. Rib groove. On some eucardiids, there may be a faint depression running down the middle of the rib; this depression is homologous to a rib interspace in Cretaceous eucardiids. States: (0) absent, (1) present.

33. Cross-striae: (0) absent, (1) present.

34. Spine morphology (Figs. 17–21). *Sche-*

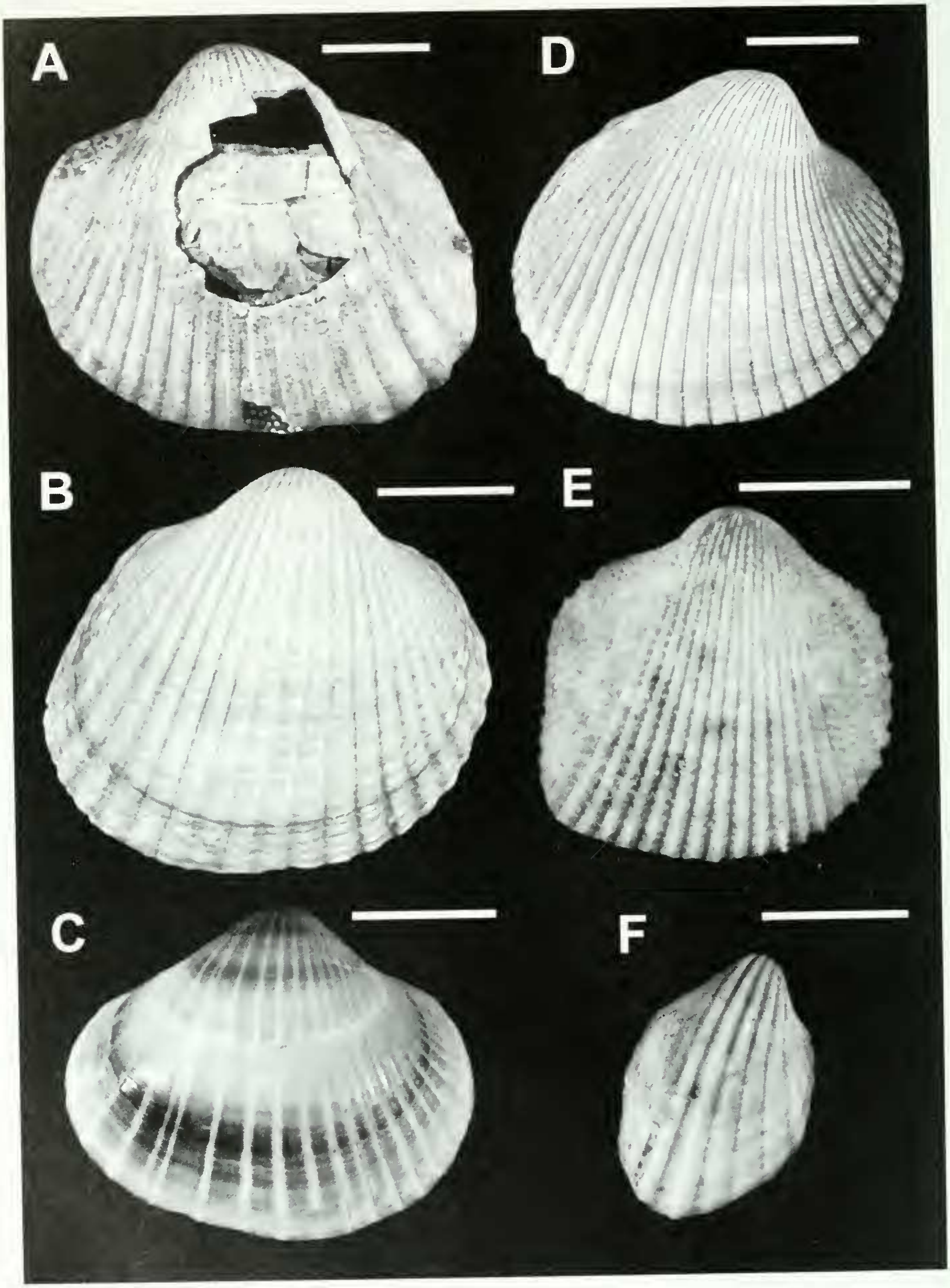

FIG. 16. Shell shape. A, *Acanthocardia (Schedocardia) hatchetigbeense*, left valve (USNM 645087 syntype); schediform. B, *Cerastoderma edule*, right valve (FMNH 278010); cerastiform. C, *Hypanis* (*Monodacna*) *colorata*, right valve (ANSP 338065); hypaniform. D, *Clinocardium nuttallii*, right valve (FMNH 278016); oval. E, *Ctenocardia symbolica*, right valve (ANSP 229980); quadrate-short. F, *Apiocardia obovale*, right valve (ANSP 317706); trigonal. A-C, E, F, scale bars = 10 mm; D, scale bar = 20 mm.

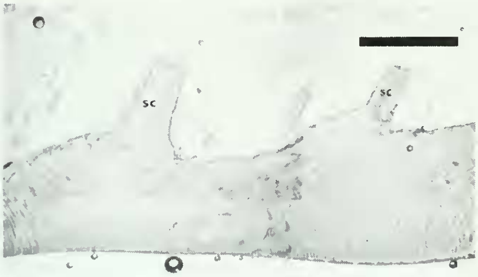

FIG. 17. Radial section through central portion of a rib of *Tridacna* (*Chametrachea*) *maxima* (FMNH 156836, right valve) to illustrate shell microstructure. Direction of ventral margin toward right, direction of umbo toward left. Note how scutes (sc) are microstructurally continuous with shell. Scale bar = 1 mm.

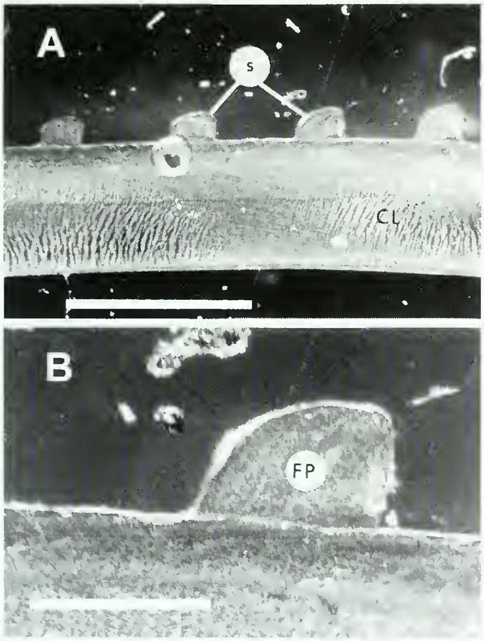

FIG. 18. Radial section through a portion of a rib of *Fragum fragum* (ANSP 288688, right valve). Note microstructural relationship of ornament to underlying shell and compare to *Granocardium kuemmeli* and *Profragum praecurrens* (Schneider, 1998: fig. 9). A, scale bar = 1 mm. B, detail of individual ornament, scale bar = 0.25 mm.

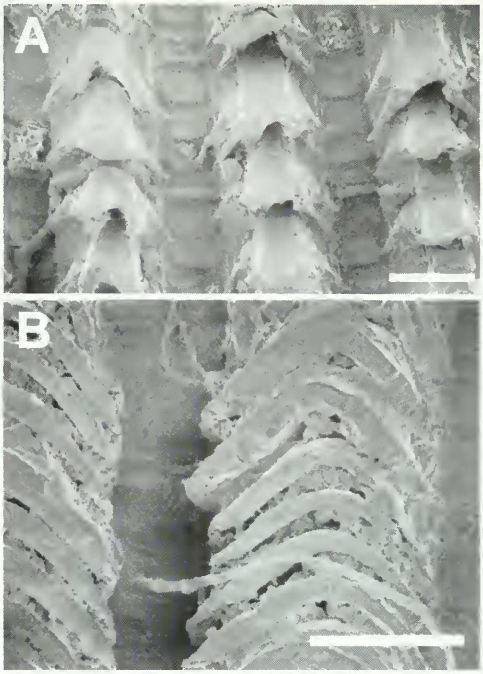

FIG. 19. External ornament of A, *Ctenocardia symbolica* (ANSP 229980, right valve), scale bar = 0.4 mm; and B, *Americardia media* (ANSP 54280, right valve), scale bar = 1 mm.

docardia (the conchological component of the outgroup) has simple spines (state 1); tridacnines and *Goethemia* have scutes (sc; state 2) (Schneider, 1998). Fraginae have poorly organized fibrous prisms (FP) microstructurally discontinuous with the underlying shell (state 3). *Maoricardium* and *Plagiocardium* (state 4) have complex spines in which the core of the spine is poorly organized fibrous prisms microstructurally discontinuous with the shell (i.e., state 3) and the outer portion of the spine is simple (state 1). Taxa lacking spines are assigned state 0.

35. Lunule flap (1f; Figs. 22A, H, 23A, H). On some cardiids, the inner shell layer may be raised just anterior to the beak; on a few forms, this structure may be reflected over the lunule and touch the beak. Although this structure has been noted numerous times in species descriptions, its phylogenetic utility was not recognized until Kafanov & Popov (1977) and Kafanov (1980) used it as one of the characters differentiating Clinocardiinae from Cardiinae. On most cardiines, the lunule flap touches the beak and is frequently reflected over the lunule. This state is unknown on clinocardiines. On clinocardiines, the lunule flap may be raised or may block the beak, but never touches it. Tridacnines are scored missing for this character, for the

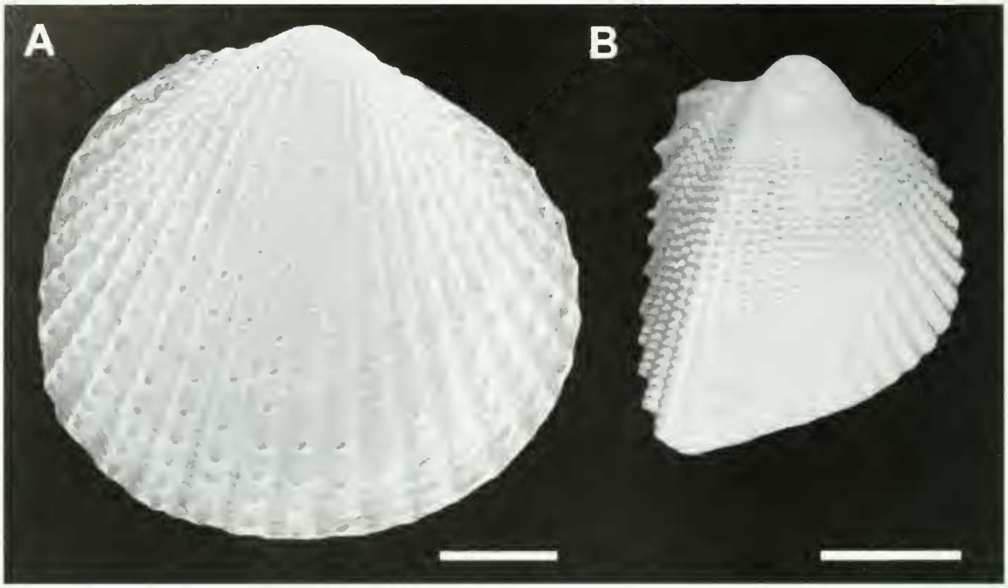

FIG. 20. External ornament of A, *Papillicardium papillosum,* right valve (ANSP 54266), scale bar = 2 mm; and B, *Fragum fragum,* right valve (ANSP 288688), scale bar = 10 mm.

lunule flap is a structure of the anterior part of the shell, which is missing in tridacnines (except for *Goniocardium*).

The terminology for this morphological structure in cardiid bivalves has never been standardized. It is here designated the lunule flap. States: (0) absent, (1) raised, does not block beak, (2) blocks beak, (3) touches beak.

36. Byssal gape (bg; Schneider, 1998; Figs. 25, 27–30). Except for *Goniocardium*, all tridacnines have a byssal gape sometime during ontogeny. This character is not redundant on the presence of a byssus (character 24), for fragines have a functional byssus but do not have a byssal gape. States: (0) absent, (1) present.

37. Riblets (rbl; Figs. 26-30). As defined by Rosewater (1965), riblets are secondary radial folds that occur on top of (1) primary radial folds and (2) between primary radial folds. The terms “primary” and “secondary” here are not used in a phylogenetic sense, but in a morphological one: the primary folds are more pronounced than the secondary ones. Riblets are found on the extant taxa of tridacnines. States: (0) absent, (1) present.

38. Pseudocarina (ps; Figs. 24, 25) Except for *Goniocardium,* tridacnines have a break in the slope of the shell that begins at the umbo and continues down that portion of the shell that is furthest from the hinge and ligament. This portion of the shell would be ventral in life condition, bearing the byssal gape. (Stasek [1962] called this portion of the shell the ventral margin. Rosewater [1965] called this portion of the shell “posterior.”) In *Avicularium* and *Byssocardium,* this slope break is strong throughout ontogeny (state 1): about 80° on *Avicularium,* and 90° on *Byssocardium.* On other tridacnines, this slope break decreases in strength through ontogeny. *Hippopus* has a slope break comparable to that of *Avicularium* and *Byssocardium* until late in ontogeny, when the angle decreases to about 60° (state 2). *Chametrachea* (state 3), *Tridacna* (*Tridacna*) (state 4), and *Persikima* (state 5) have sequentially weaker slope breaks and earlier onset of the decrease in strength of the slope break. Therefore, this character can be linearly ordered on the basis of ontogeny. This character satisfies Alberch's (1985) criterion, because the angle of the pseudocarina at time 1 would depend upon the angle of the pseudocarina at time 0. Taxa lacking a pseudocarina are scored absent (state 0), which is considered primitive on the basis of outgroup comparison.

This structure is herein called the pseudocarina. It should not be called a carina, for a true carina refers to a change in the angle on the surface of a shell, demarcating the posterior slope of the shell from the central slope. A

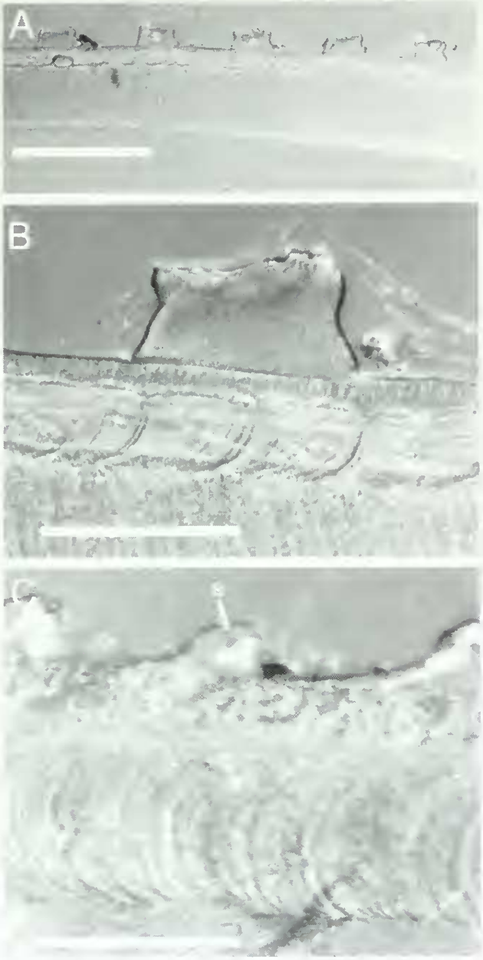

FIG. 21. Microstructure of ornament of *Maoricardium pseudolatum* (ANSP A103, right valve). A, B, radial section through central portion of ornament. Note that ornament is microstructurally discontinuous with underlying shell. C, radial section through side of ornament. Note that ornament is microstructurally continuous with underlying shell. A, scale bar = 2 mm; B, scale bar = 0.5 mm; C, scale bar = 0.2 mm.

carina is prominent in fragines (Kafanov & Popov, 1977), especially *Corculum*. Keen (1980) referred to the fragine carina as an umbonal ridge. Voskuil & Onverwagt (1989) referred to this structure on *Ctenocardia* and *Parvicardium* as an umbonal keel. Because the slope break on tridacnines does not demarcate the posterior slope from the central slope, it is not homologous to the carina.

B. Muscle scars

39. Dorsoumbonal scar. This muscle scar indicates the attachment point of the pedal elevator muscle, which is present in virtually all cardiids (Pelseneer, 1911; Cox, 1969; Kafanov, 1980). In some clinocardiines, the scar is more deeply impressed into the shell and more darkly colored than in other cardiids. Because the pedal elevator muscle is more firmly attached in these forms, it takes greater effort to remove an animal for dissection. Furthermore, when the pedal elevator muscle is separated from the dorsoumbonal muscle scar, there is an audible ripping sound. States: (0) weak, (1) strong.

40. Adductor muscle scars (Fig. 32): (0) anterior and posterior adductor muscle scars roughly equal in size and equally distant from shell margin, (1) anterior adductor muscle scar smaller, much closer to shell margin; posterior adductor muscle scar larger, located further from shell margin, (2) anterior muscle scar absent, posterior adductor muscle scar large and located in central portion of shell.

C. Ligament groove and nymph

41. Ligament groove on right valve (Fig. 22). On the right valves of *Clinocardium, Keenocardium, Fuscocardium, Serripes* and *Yagudinella,* the ligament (lg) groove is continuous with the posterior lateral socket (pls). On all other cardiids, the ligament groove terminates anterior of the posterior lateral socket. States: (0) not continuous with posterior lateral socket, (1) continuous with posterior lateral socket.

42. Nymph (n; Figs. 22, 23): (0) not located immediately dorsal to cardinal teeth, (1) located immediately dorsal to cardinal teeth.

D. Hinge (Figs. 22, 23). Tridacnines, excluding *Goniocardium*, plus the lymnocardiines *Hypanis* and *Didacna*, have no anterior lateral teeth and are therefore scored missing (?) for characters 44–47. *Hypanis* and *Didacna* lack posterior laterals, and are scored missing for character 48. *Byssocardium* and the extant tridacnines lack the anterior cardinal tooth and are scored missing for character 49.

43. Posterior umbonal buttress (pub). On some cardiids, the hinge plate is raised just posterior of the beak, blocking the beak. States: (0) absent, (1) present.

44. Right anterior ventral lateral tooth (vlt) (0) does not continue into umbo, (1) does continue into umbo. Dall (1903) noticed that for some cardiids "the teeth often . . . seem to

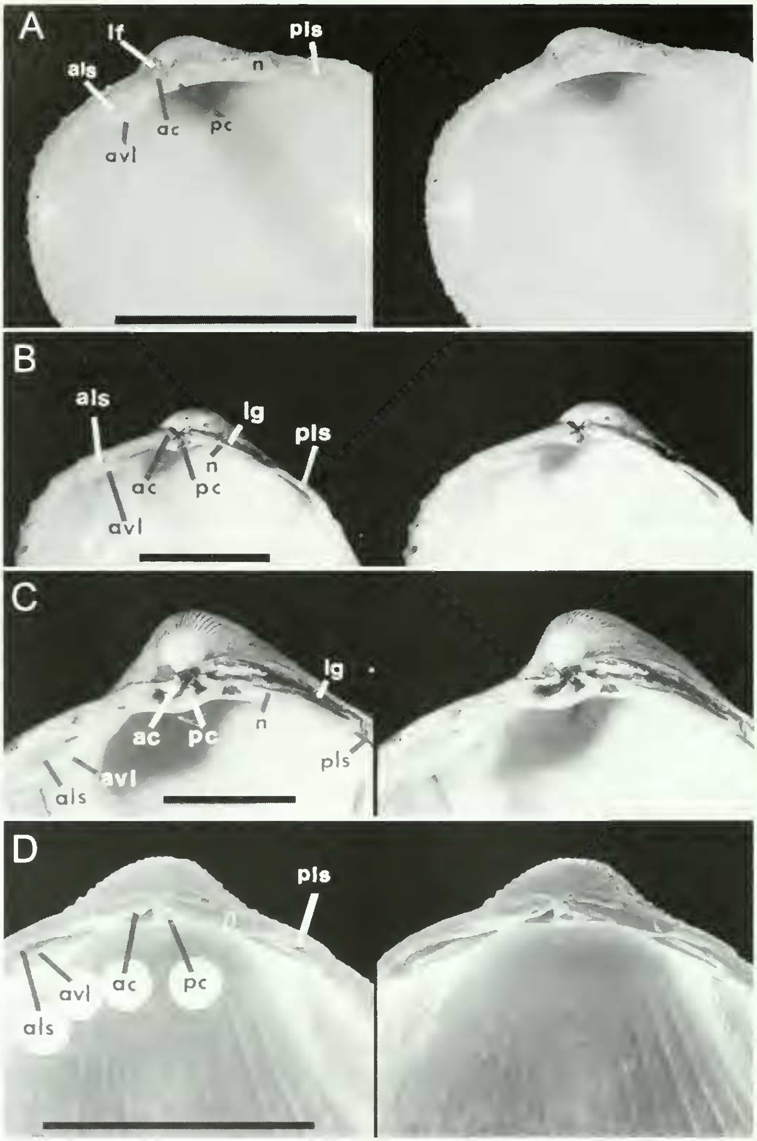

FIG. 22. Right hinges, stereo pairs. A, *Maoricardium pseudolatum* (ANSP A103), scale bar = 20 mm. Left pls moderate, ac shape 1, pc shape 1. B, *Ciliatocardium ciliatum* (ANSP 54269), scale bar = 20 mm. Left pls moderate, ac shape 1, pc shape 1. C, *Clinocardium nuttallii* (FMNH 278016), scale bar = 20 mm. Left pls moderate, ac shape 2, pc shape 1. D, *Papillicardium papillosum* (ANSP 54266), scale bar = 10 mm. Left pls absent, ac shape 3, pc shape 1. E, *Parvicardium exiguum* (ANSP 54289), scale bar = 1 mm. Left pls small, ac shape 3, pc shape 2. F, *Trigoniocardia antillarum* (ANSP 283822), scale bar = 3 mm. Left pls large, ac shape 3, pc shape 3. G, *Goniacardia callopleura* (ANSP 3445), scale bar = 3 mm. Left pls large, ac shape 3, pc shape 3. H, *Fragum fragum* (ANSP 288688), scale bar = 10 mm. Left pls large, ac shape 3, pc shape 3. I, *Ctenocardia symbolica* (ANSP 229980), scale bar = 5 mm (Fig. 22), = 2 mm (Fig. 23). Left pls moderate, ac shape 3, pc shape 3. J, *Americardia media* (ANSP 54280), scale bar = 10 mm (Fig. 22), = 5 mm (Fig. 23). Left pls moderate, ac shape 3, pc shape 3. K, *Corculum cardissa* (ANSP 231526), scale bar = 10 mm. Left pls absent, ac shape 4, pc shape 5. L, *Cerastoderma edule* (FMNH 278010), scale bar = 17 mm. Left pls moderate, ac shape 3, pc shape 1. M, *Hypanis* (*Monodacna*) *colorata* (ANSP 338065), scale bar = 10 mm. No posterior laterals (left pls coded as missing, "?"), ac shape 3, pc shape 1. N, *Goethemia elegantula* (SMNH 883), scale bar = 1 mm. Left pls absent, ac shape 3, pc shape 1. O, *Avicularium aviculare* (ANSP 6279), scale bar = 10 mm. Left pls small, ac missing (coded "?"), pc shape 2. P, *Byssocardium emarginatum* (IRSNB I. G. 10591), scale bar = 13 mm. Left pls small, ac missing, pc shape 2. Q, *Tridacna* (*Chametrachea*) *maxima* (ANSP 252683), scale bar = 90 mm. Left pls absent, ac missing, pc shape 2.

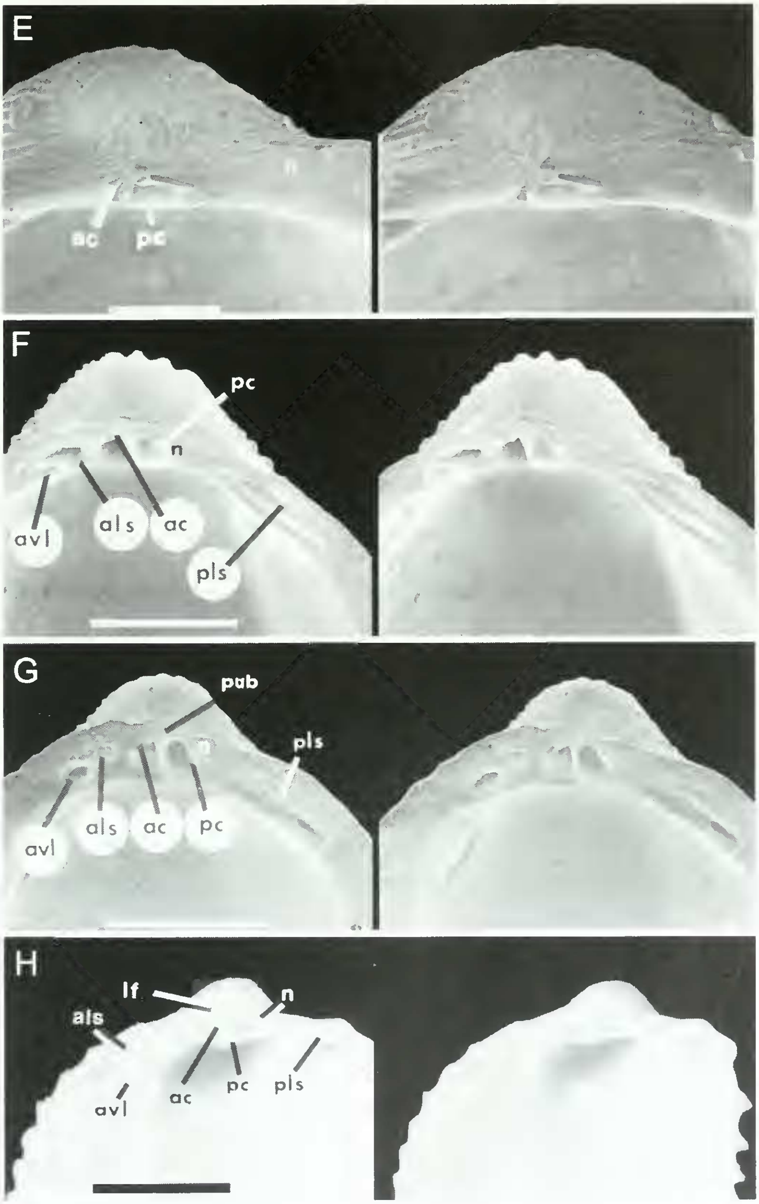

FIG. 22. Continued.

spring from the umbonal cavity rather than from a hinge plate . . ."

45. Right anterior ventral lateral tooth: (0) does not insert into anterior lateral socket, (1) inserts into anterior lateral socket.

46. Left anterior lateral (al) (0) not horizontal, (1) horizontal.

47. Left anterior lateral socket (als): (0) absent or small, (1) large.

48. Left posterior lateral socket (pls): (0) absent or small, (1) moderate, (2) large.

49. Right anterior cardinal (ac) shape: states 0 to 4.

50. Right posterior cardinal socket angle:

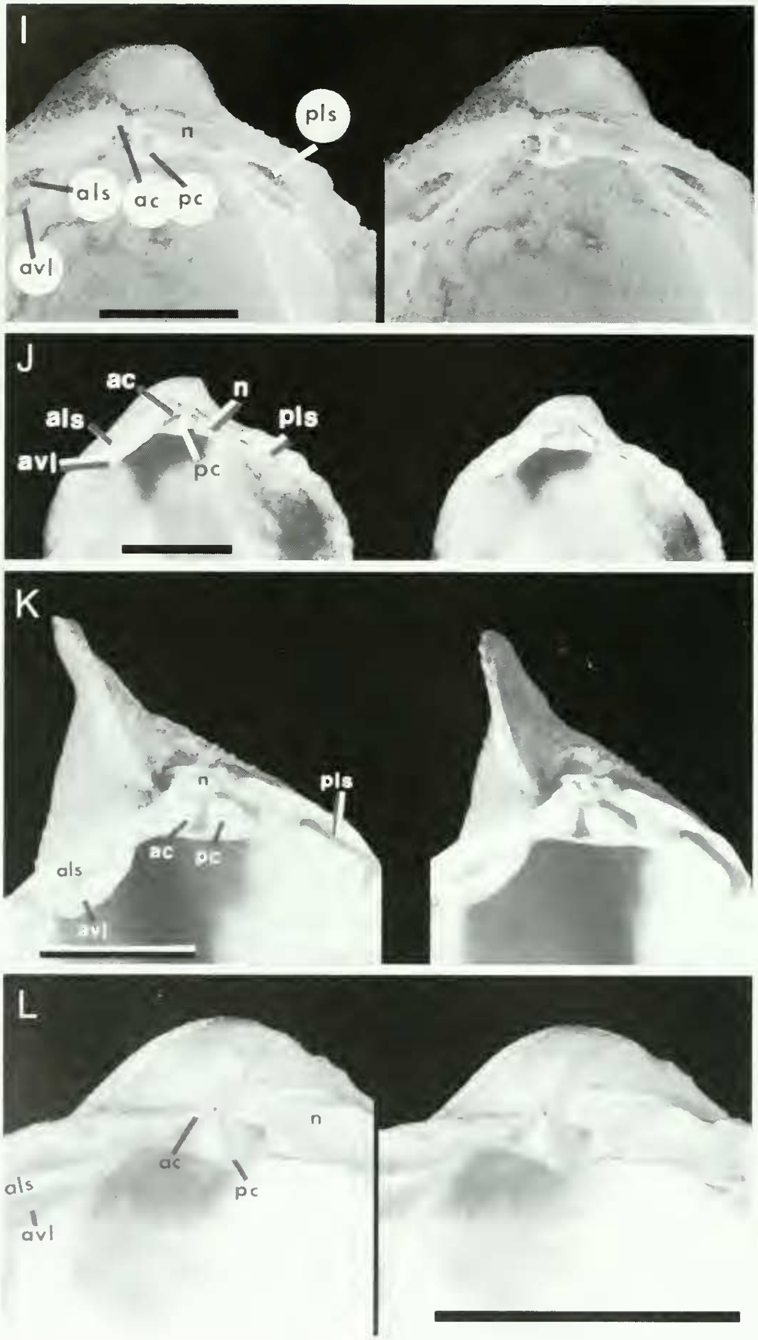

FIG. 22. Continued.

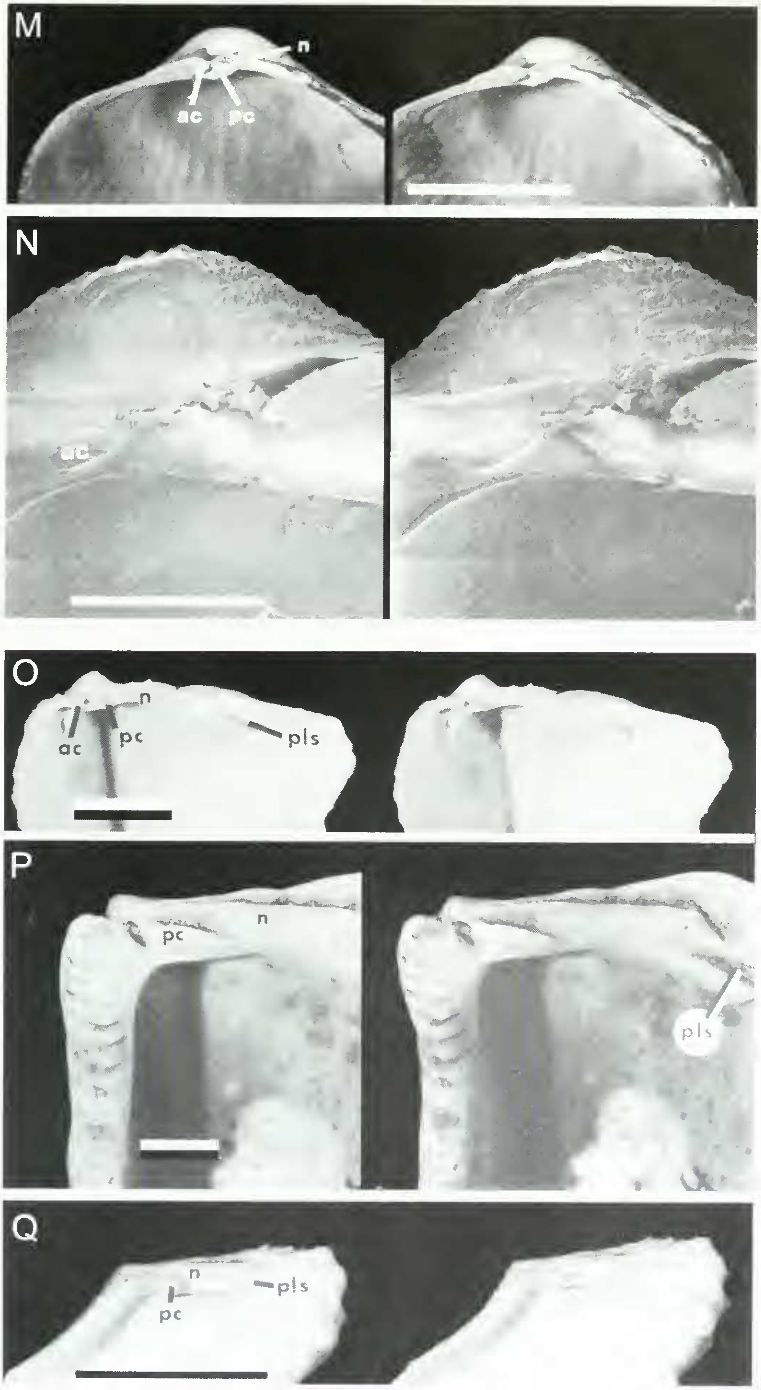

FIG. 22. Continued.

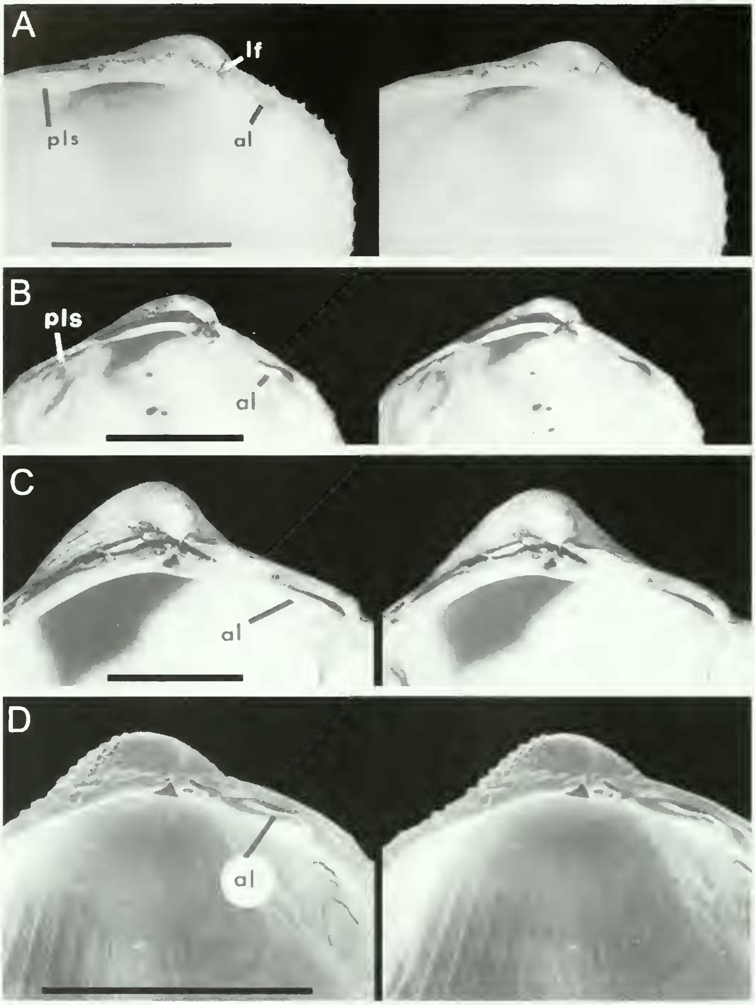

FIG. 23. Left hinges, stereo pairs. For explanation, see caption to Figure 22.

(0) high (>40° from horizontal), (1) low (<40° from horizontal).

51. Right posterior cardinal (pc) shape: states 0 to 5

RESULTS

PAUP 3.1.1 found 28 most parsimonious trees of length 162 steps (CI = 0.605, RI = 0.805). The majority-rule consensus tree is presented in Figure 33. Syanapomorphies for internal nodes of tree number 15 are presented in Figure 34 and Table 2. A suggested taxonomy of the ingroup is presented in Table 3. The taxonomies of Keen (1969a, b, 1980) and Popov (1977; Kafanov & Popov, 1977) are presented in Appendices 4 and 5.

The ingroup has a topology of (*Plagiocardium* (*Maoricardium* + and all other taxa)). *Plagiocardium* was found to be a member of the Fraginae by Kafanov & Popov (1977) and Schneider (1992). Clinocardiinae contains the same taxa included in the group by Kafanov (1980). Kafanov considered *Fuscocardium* a subgenus of *Clinocardium*, and the genus *Keenocardium* the closest relative of these two taxa. Along with *Ciliatocardium*, Kafanov

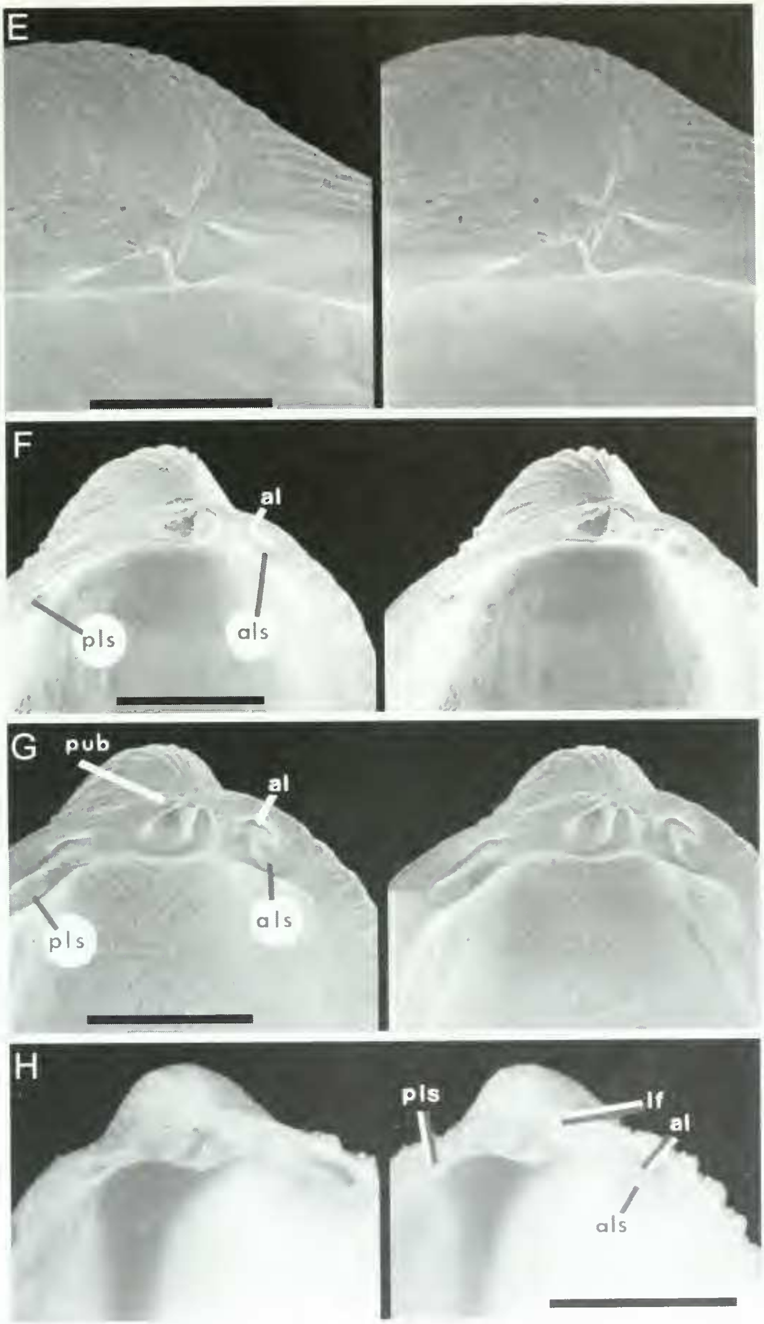

FIG. 23. Continued.

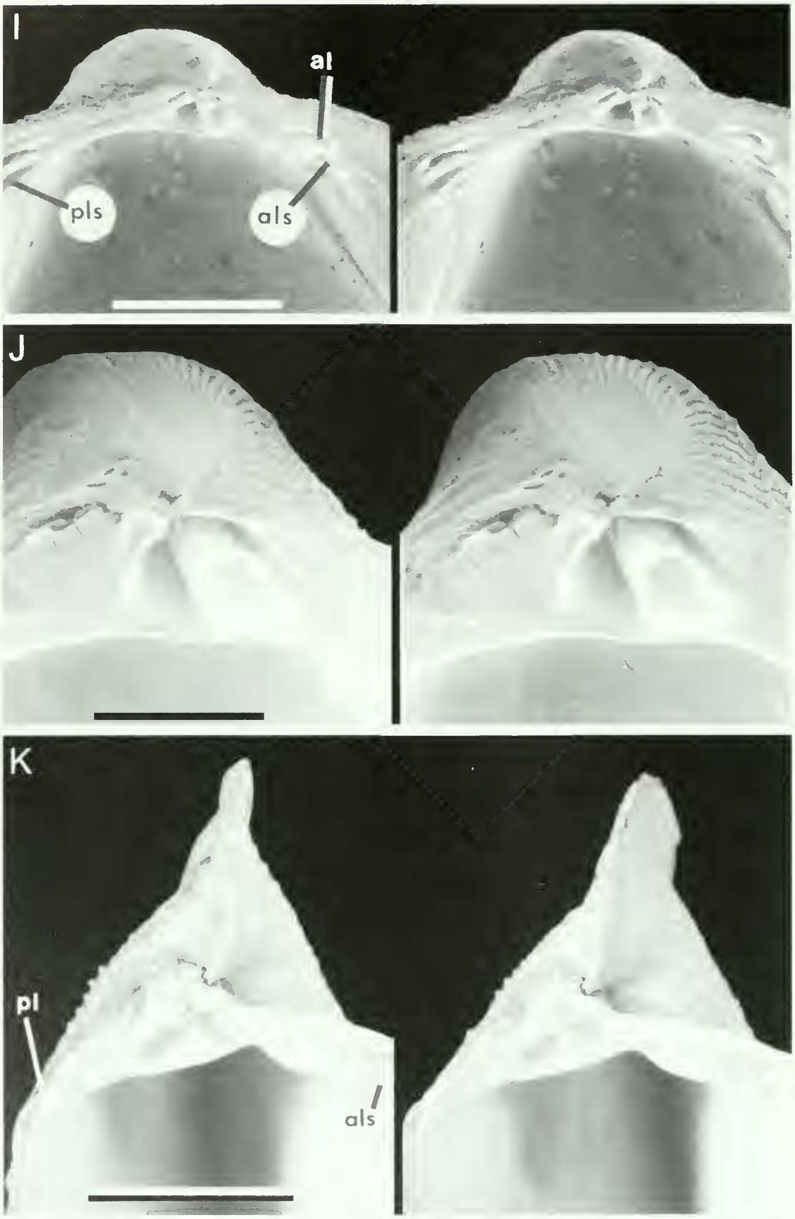

FIG. 23. Continued.

placed these taxa in the tribe Clinocardiini. In the present analysis, *Ciliatocardium* is most closely related to *Profulvia*, the only genus that Kafanov (1980) placed in the tribe Profulviini. Kafanov (1980) placed *Serripes* and *Yagudinella* in the tribe Serripedini.

Goethemia is the sister group to Lymnocardiinae + Tridacninae, and these three taxa together are the sister group to Fraginae. Lymnocardiinae *sensu* Kafanov & Popov (1977) (i.e., including *Cerastoderma*), Tridacninae, and Fraginae are monophyletic groups. Cerastodermatiinae *sensu* Nordsieck (1969) and Voskuil & Onverwagt (1989) would be a para-

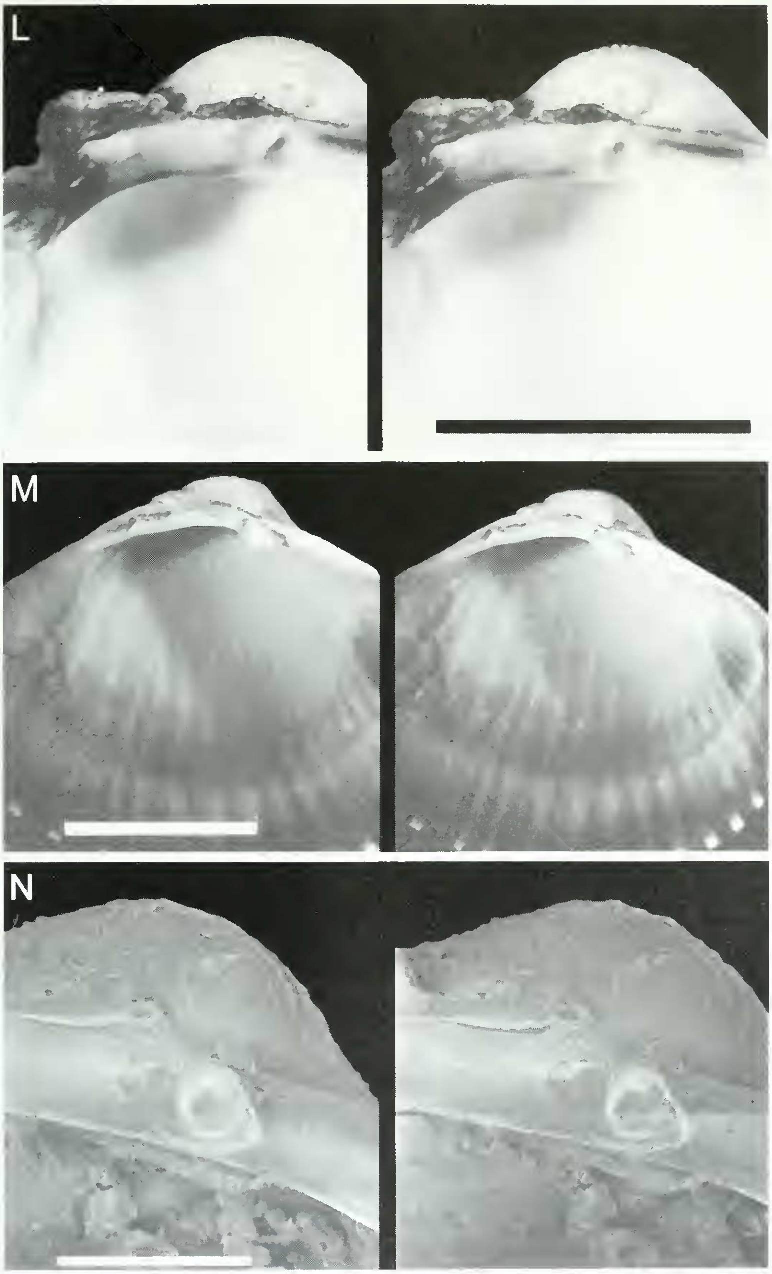

FIG. 23. Continued.

phyletic group, specifically a grade containing basal fragines (*Parvicardium*, *Papillicardium*, and *Cerastobyssum*), the sister taxon to Lymnocardiinae + Tridacninae (*Goethemia*), and a basal lymnocardiine (*Cerastoderma*).

Papillicardium is the sister taxon to the remaining fragines. *Papillicardium* should be considered a genus as opposed to a subgenus of *Parvicardium*.

All the most parsimonious trees support a

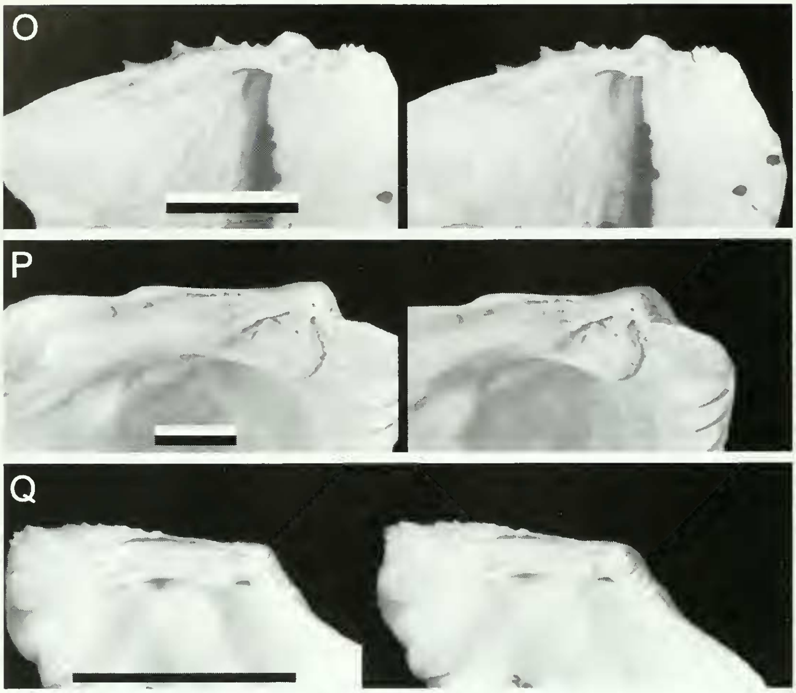

FIG. 23. Continued.

monophyletic group of *Trigoniocardia*, *Apiocardia*, and *Goniacardia* (the "*Trigoniocardia*-group"). *Apiocardia* and *Goniacardia* are considered subgenera of *Trigoniocardia* by Olsson (1961), Keen (1969a, 1980), Woodring (1982), and Vokes (1989).

All the trees support a clade of (*Microfragum* + (*Ctenocardia* + *Americardia*)), which can informally be referred to as the *Ctenocardia*-group. *Microfragum*, erected as a genus by Habe (1951), was considered a subgenus of *Ctenocardia* by Keen (1969a, 1980). On the basis of the hinge, Wilson & Stevenson (1977) considered *Microfragum* a subgenus of *Fragum*. *Americardia* was erected as a subgenus of *Trigoniocardia* by Stewart (1930), who was followed by Clench & Smith (1944), Keen (1951, 1969a, 1980), Olsson (1961), Glibert & van de Poel (1970), and Popov (1977). Woodring (1982) and Vokes (1989) raised *Americardia* to genus. Voskuil & Onverwagt (1989) synonomized *Americardia* with *Ctenocardia*.

All most parsimonious trees support a sister taxon relationship of *Lunulicardia* and *Corculum*, which agrees with Popov's (1977) treatment of *Lunulicardia* as a subgenus of *Corculum*. Keen (1969a, 1980) had considered *Lunulicardia* a subgenus of *Fragum*. In the present analysis, *Fragum* is one branch of a trichotomy with the *Ctenocardia*-group and *Lunulicardia* + *Corculum*.

DISCUSSION

Plagiocardium and *Maoricardium*

Plagiocardium and *Maoricardium* display several features that seem to be intermediate in morphology between basal eucardiids (subfamilies Profraginae, Trachycardiinae and Cardiinae; see Schneider [1993a, 1995] for a definition of eucardiids) and the more derived eucardiids (the remainder of the ingroup). *Cardium ciliatum* Fabricius, 1780, the type species of *Ciliatocardium*, was named for the presence of periostracal cilia (27:1). Since Reeve (1844), periostracal cilia have been known from what are now considered the Recent species of *Maoricardium*. To my knowledge, the possibility that the periostracal cilia

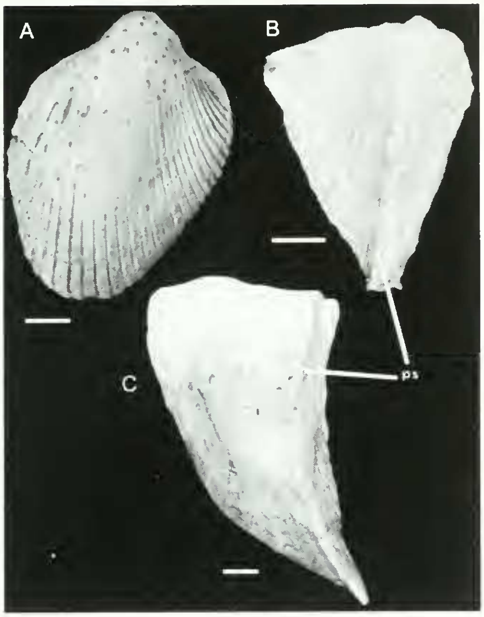

FIG. 24. External views of right valves of extinct tridacnines. A, *Goniocardium rachitis* (ANSP 12429). B, *Avicularium aviculare* (ANSP 6279). C, *Byssocardium emarginatum* (IRSNB I. G. 10591). Scale bars = 5 mm. All have trigonal shell shape, which is considered derived from trigonal shell shape (see shell shape key in Schneider, 1998).

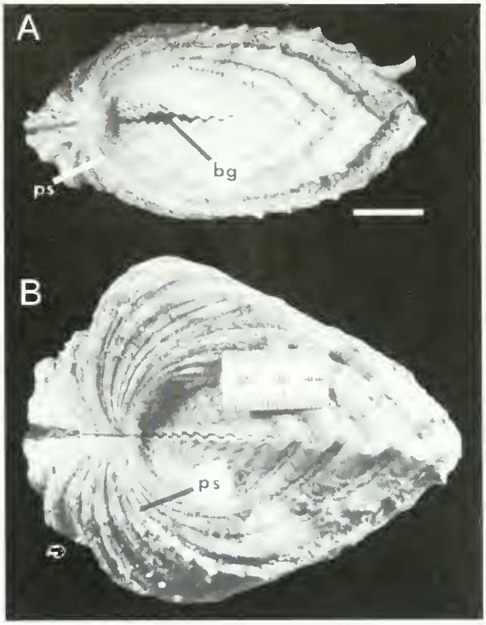

FIG. 25. *Hippopus hippopus*. A, juvenile (USNM 63793) with byssal gape, scale bar = 10 mm. B, adult (USNM 621313) with no byssal gape, scale indicated in figure.

of these two taxa are homologous has not previously been suggested. Clinocardiines have the same shape right posterior cardinal (51:1) as *Plagiocardium* and *Maoricardium*. The basal clinocardiines, *Ciliatocardium* and *Profulvia*, have the same shape right anterior cardinal (49:1) as *Plagiocardium* and *Maoricardium*. Kafanov & Popov (1977) were uncertain of how the subfamily Clinocardiinae was related to other cardiids. Kafanov & Savitskiy (1982) suggested that clinocardiines were derived from trachycardiines, for the earliest member of the subfamily (*Ciliatocardium asagaiense* [Makiyama, 1934], Early Oligocene of Sakhalin and Japan) has rudimentary ornament on the radial ribs. However, *Plagiocardium* and *Maoricardium* also have ornament on the radial ribs.

According to the results, the characters shared by *Plagiocardium* and *Maoricardium* on one hand, and Clinocardiinae on the other, are either symplesiomorphic (shape of cardinal teeth, shell shape) or homoplastic (periostracal cilia). Postulating that the periostracal cilia of *Maoricardium* and clinocardiines are homologous (i.e., symplesiomorphic, having been derived only once and subsequently lost twice) would add one step to the most parsimonious trees.

The ornamental microstructure of basal eucardiids is simple knobs, comprised of branching crossed lamellae grading into fibrous prisms, in microstructural continuity with the rest of the shell (Schneider, 1998). The ornamental microstructure of members of the subfamily Fraginae consists of poorly organized fibrous prisms that are microstructurally discontinuous with the shell (Fig. 18). In *Plagiocardium* and *Maoricardium*, the core of a spine is the poorly organized fibrous prisms that are microstructurally discontinuous with the shell (Fig. 21). However, the outer portion of the spine is somewhat more organized fibrous prisms, which are not microstructurally discontinuous with the branching crossed lamellae of the shell. This microstructure appears to be that of simple spines (Schneider, 1998: fig. 9). According to the results of the cladistic analysis, *Plagiocardium*, *Maoricardium* and Fraginae independently evolve this discontinuity. Postulating that this shell-spine discontinuity is homologous between *Plagiocardium* + *Maori-*

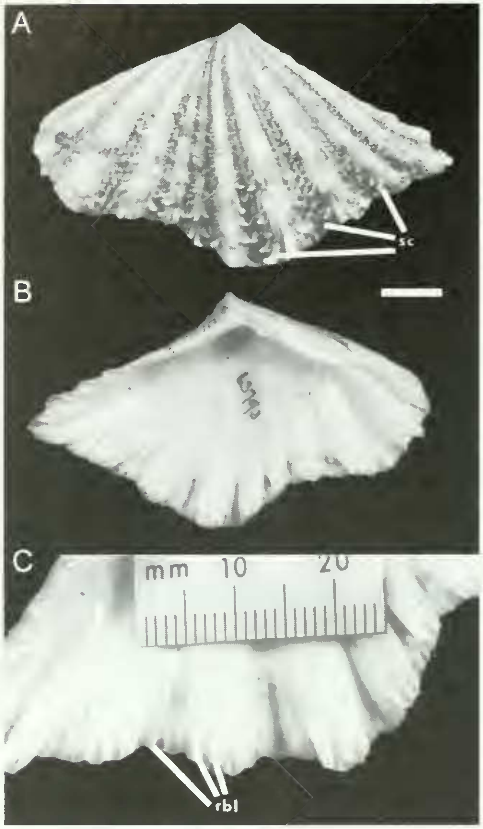

FIG. 26. *Hippopus hippopus*. A-C, juvenile (USNM 63793), right valve. A, external. Note scutes on "riblets". B, internal. Scale = 10 mm. Note expression of "riblets" at ventral margin. C, detail of B, scale indicated in figure.

cardium on one hand, and Fraginae on the other, would add one step to the most parsimonious trees.

Given the foregoing, the phylogenetic relationships of *Plagiocardium* and *Maoricardium* are uncertain, and the naming of new subfamilies is strongly discouraged at this time. It is altogether possible that *Plagiocardium* and/or *Maoricardium* are paraphyletic, and species assigned to these taxa in the literature are actually basal members of other subfamilies.

Morphological Evolution of Clinocardiinae

Much of the morphological evolution of the Clinocardiinae involves modification of the foot, its musculature, and the attachment of these muscles to the shell. These characters

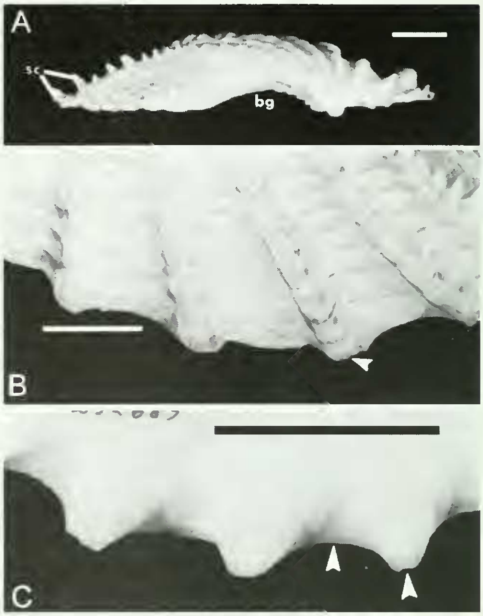

FIG. 27. *Tridacna* (*Chametrachea*) *maxima*. A-C, juvenile (ANSP 252683), right valve. A. View of byssal gape. B. Ventral margin. Note scutes and expression of "riblets" (indicated by arrow) at ventral margin. C. Internal view of ventral margin. Note expression of "riblets", indicated by arrows. Scale bars = 10 mm.

are (1) ventral papillae on the foot (8:1), (2) the strength of the dorsoumbonal muscle scar (39:1), which is the attachment site of the pedal elevator muscle (Pelseneer, 1911; Cox, 1969), and (3) the degree of umbonal prosogyry (29:1). Increase in prosogyry results in an increase of the length of the pedal elevator muscles. These characters are independent since they do not have the same distribution among clinocardiines. Ventral papillae are present on all clinocardiines. Kafanov (1980) stated that papillae are absent on *Keenocardium*. However, I have detected microscopic appendages on *Keenocardium*. *Trigoniocardia* + *Apiocardia* + *Goniacardia* independently derives ventral papillae. The dorsoumbonal muscle scar is weak in the primtive clinocardiine *Ciliatocardium* (state unknown in its sister taxon *Profulvia*).

Systematics and Evolution of Giant Clams (Tridacninae)

The giant clams form a monophyletic group within the family Cardiidae and therefore

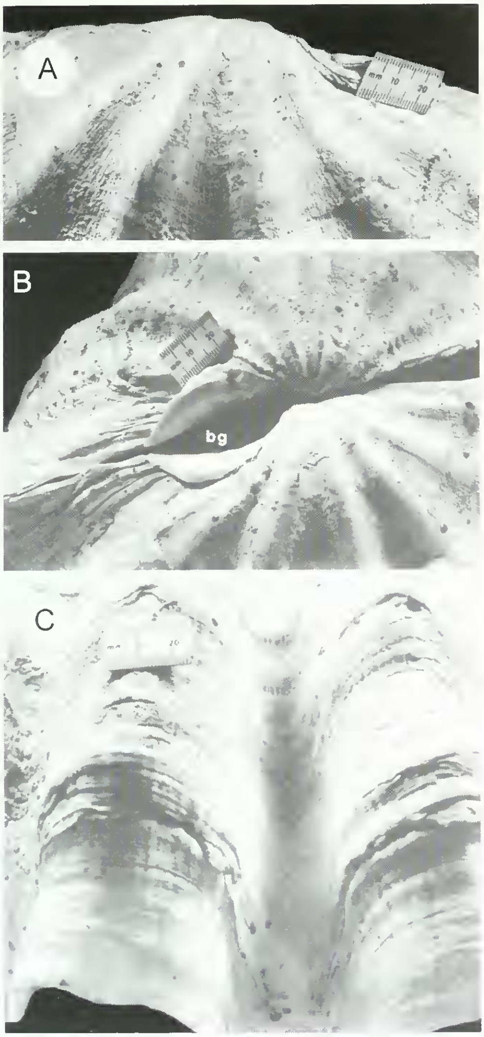

FIG. 28. *Tridacna gigas*. A-C, adult (USNM 602502). A, umbo of right valve. Note "riblets", manifested as radial striations running from the umbo towards the ventral margin. B, detail of narrow byssal gape. C, ventral margin of right valve. Note faint expression of "riblets". Scales indicated in figure.

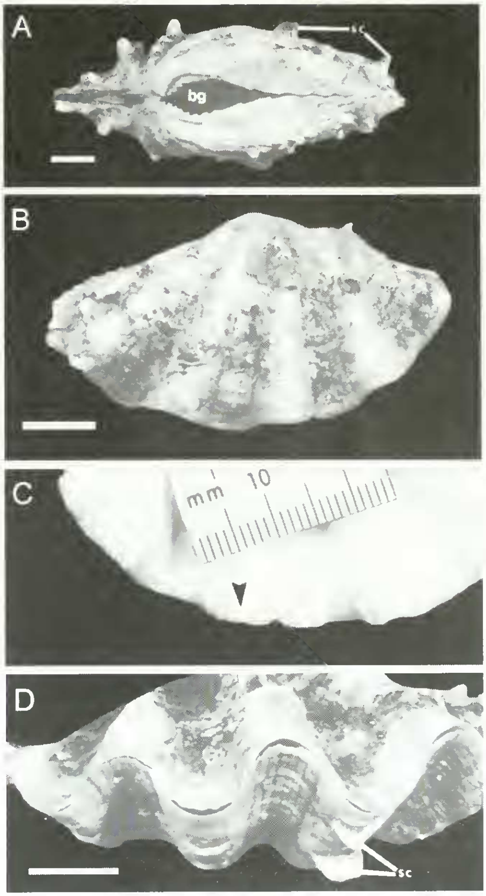

FIG. 29. *Tridacna gigas*. A-D, juvenile (USNM 686575). A, view of large byssal gape (compare with Fig. 31B) and scutes. B, external view of right valve. C. Internal view of ventral margin (same specimen as in B). Note expression of "riblets" as crenulations at margin, indicated by arrow. D. Commissure. Note scutes and "riblets". A, B, D, scale bar = 10 mm; C, scale indicated in figure.

should be considered a subfamily (Tridacninae) of Cardiidae. Keeping the giant clams as a separate family (Fischer, 1887; Ridewood, 1903; Zittel, 1927; Thiele, 1934; Yonge, 1936, 1953a, b, 1981, 1982), or even superfamily (Kafanov & Popov, 1977; Scarlato & Starobogatov, 1979; Purchon, 1987a, b; Keen, 1969b; and *The Zoological Record*) makes the Cardiidae a paraphyletic group. Lamarck (1809) was the first to recognize a close relationship between cardiids and giant clams. Noting the similarities of the hinge, Yonge (1936) thought that the giant clams were derived from a *Cerastoderma*-like form. The results of the cladistic analysis indicate a sister taxa relationship between Tridacninae and Lymnocardiinae. Because *Cerastoderma* is the least derived lymnocardiine, Yonge's view is upheld.

Much of the evolutionary history of giant clams had been understood by the middle of the twentieth century. A step backwards in our

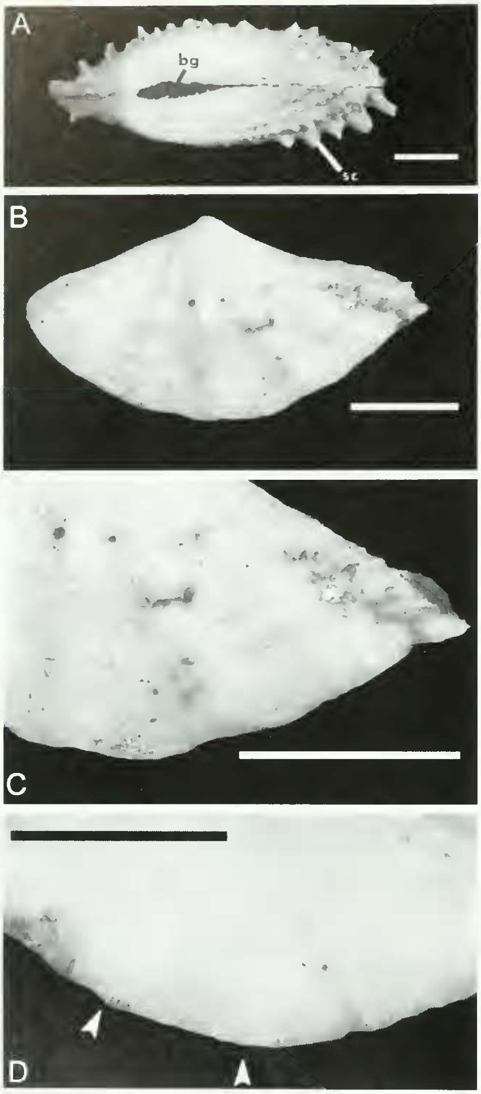

FIG. 30. *Tridacna (Persikima) derasa*. A-D, juvenile (USNM 845538). A, view of byssal gape; note prominent scutes. B, C, external view of right valve. Note weak expression of "riblets" on shell exterior. D, Internal view of ventral margin (same specimen as in B and C). Note weak expression of "riblets" as crenulations along interior ventral margin, indicated by arrows. Scale bars = 10 mm.

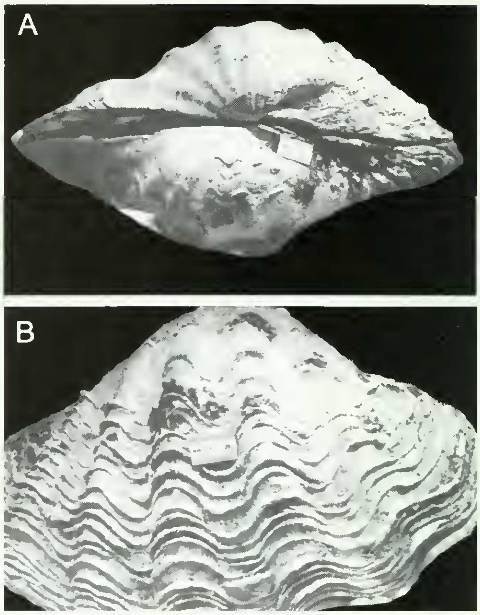

FIG. 31. *Tridacna derasa*. Adult (USNM 654256), A, B, scales indicated in figures. A, dorsal view. Note absence of byssal gape. B, external view of right valve. Note that "riblets" are not detectable on A and B.

understanding of giant clam evolution was taken when a presumably Miocene *Chametrachea* was described as coming from Cretaceous sediments. Collignon (1949) described *Tridacna besairiei* from the Maastrichtian of Madagascar. Collignon received the fossil in a box of specimens from H. Besairie. The other fossils in the box were from the Maastrichtian (later redescribed as Danian [Collignon, 1968]) zone G à *Tripylus* de Antonibe, Madagascar, and the box was labeled accordingly. Collignon (1949) took Besairie's word that *T. besairiei* was from Antonibe and noted that the nearest Miocene sediments were 150 kilometers from Antonibe. The distance from Antonibe to Miocene outcrops is irrelevant, for Besairie collected specimens from all over Madagascar, and specimens from different localities and strata may have been accidentally mixed. There is no evidence that *T. besairiei* comes from Danian sediments. Unfortunately, subsequent authors (Stasek, 1962; Rosewater, 1965; Keen, 1969b; Sepkoski, 1992) gave at least some creedence to Collignon's (1949, 1968) claim of a Maastrichtian/Danian *Tridacna*. Acceptance of a moderately derived *Tridacna* approximately 15 million years older than the more primitive forms *Goniocardium, Avicularium,* and *Byssocardium* obfuscated the actual tempo and mode of tridacnine evolution, and the correspondence between the

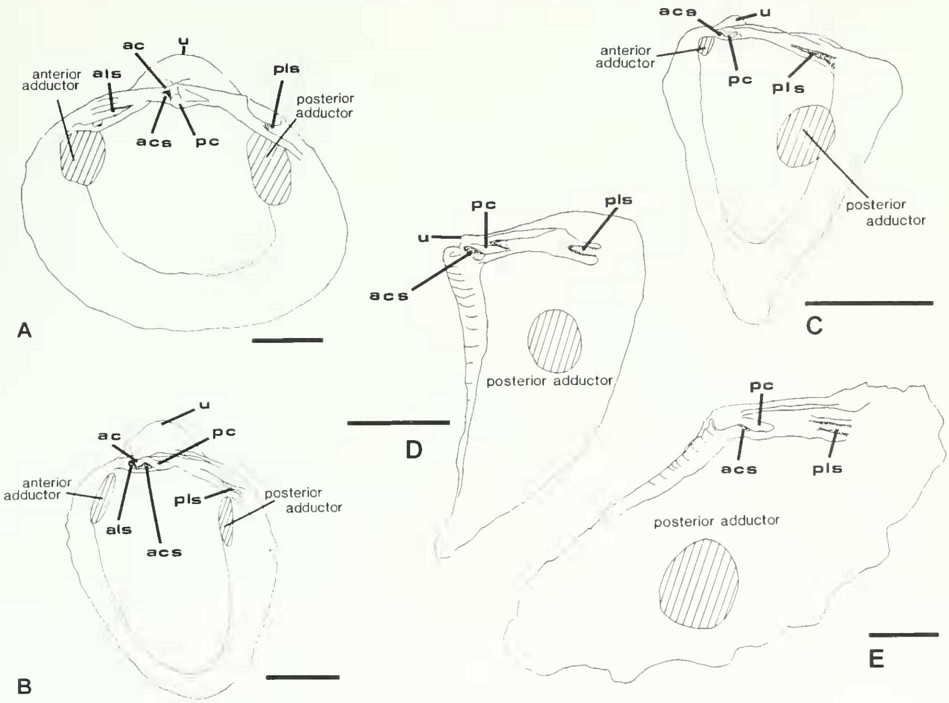

FIG. 32. Camera lucida drawings of interior of right valves of *Cerastoderma edule* and several tridacnines, to show morphology of hinge and adductor muscle scars. A, *Cerastoderma edule* (FMNH 278010). B, *Goniocardium rachitis* (ANSP 12429). C, *Avicularium aviculare* (ANSP 6279). D, *Byssocardium emarginatum* (IRSNB I. G. 10591). E, *Tridacna* (*Chametrachea*) *maxima* (ANSP 252683). A–C, E, scale bars = 10 mm; D, scale bar = 15 mm.

actual fossil record and morphological evolution has not been appreciated.

The three most basal giant clams are the extinct taxa *Goniocardium* Vasseur, 1880, *Avicularium* Gray, 1853 (= *Lithocardium* Woodward, 1854), and *Byssocardium* Munier-Chalmas, 1882. All three taxa originated in the Middle Eocene (Keen, 1969b). These taxa were erected as genera of Cardiidae (note the generic names) and comprised species that had been described under *Cardium* (Lamarck, 1819; Deshayes, 1829; Bronn, 1831; Michelotti, 1861), not *Tridacna.* However, many workers recognized that the species of *Avicularium* and *Byssocardium* were either allied to the tridacnine *Hippopus* (Sowerby, 1823; Gray, 1853) or transitional from cardiids to giant clams (Tournauer, 1882; Fischer, 1887; Grobben, 1898; Anthony, 1904, 1920; Thiele, 1934; Yonge, 1936; Dechaseaux, 1952). Deshayes (1829) criticized Sowerby for suggesting that *Cardium avicularium* (Lamarck, 1805) was related to *Hippopus* on the basis of the position of the muscle scars. Deshayes called the similarity of the muscle scars between these two taxa an "analogie trompeuse" ("false analogy"). Grobben (1898) was the first to recognize an (*Avicularium* (*Byssocardium* (Recent tridacnines))) pattern of relationships and to discuss the morphological evolution of the adductor muscle scars and byssal gape. Cossmann (1886, 1905, 1921; Cossmann & Pissarro, 1904) considered *Avicularium* and *Byssocardium* to be cardiids. Keen (1937) transferred *Avicularium* and *Byssocardium* to Tridacnidae.

The relationship of the species of *Goniocardium* to giant clams took longer to be recognized. The species of *Goniocardium* were considered cardiids by Deshayes (1829), Vasseur (1881), and Cossmann (1886, 1905, 1921; Cossmann & Pissarro, 1904). Cossmann (1886) and Koenen (1893) placed species of *Goniocardium* in *Fragum.* (The Early Oligocene species *Cardium* (*Fragum*) *reniforme* Koenen, 1893, is a *Goniocardium;* this is the first atribution of an Oligocene species to *Goniocardium.*) Dall (1903) was

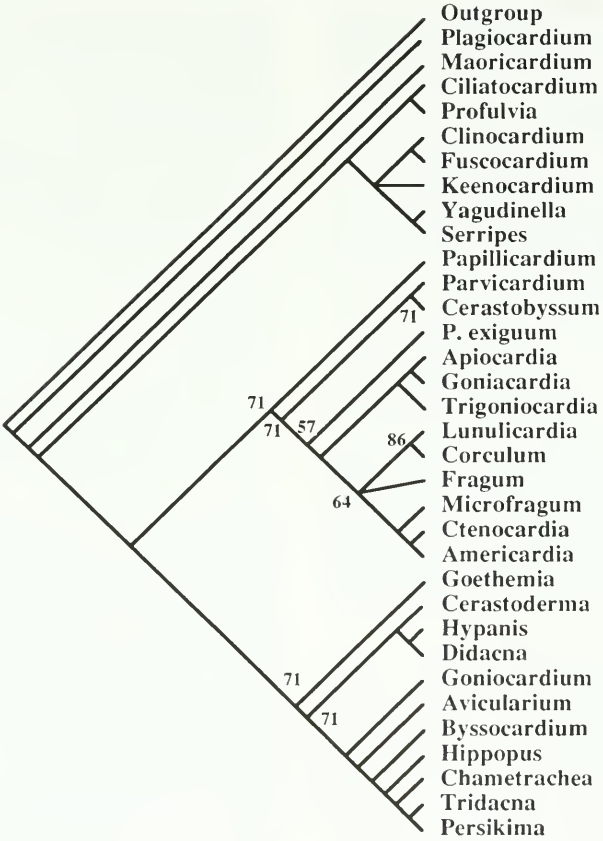

FIG. 33. Majority-rule tree of 28 most parsimonious trees. Numbers indicate percentage of trees which support that node. Unnumbered nodes supported by all 28 trees.

the first to suggest that *Goniocardium* was related to *Avicularium* and *Byssocardium,* but put all three taxa in Cardiidae. Dall did not discuss the possibility that these forms were related to tridacnids. Keen (1937) was unsure of the affinities of *Goniocardium*, suggesting a relationship to the lymnocardiine *Prosodacna.* Stasek (1962) was the first worker to realize that *Goniocardium* was morphologically intermediate between cardiids and the basal giant clams *Avicularium* and *Byssocardium.* Rosewater (1965) and Keen (1969b) followed Stasek (1962) and transferred *Goniocardium* to Tridacnidae.

In general, *Cerastoderma* has the typical cardiid hinge and muscle scar arrangement (Fig. 32A). The right valve has both anterior and posterior lateral teeth, and anterior and posterior lateral sockets. There are both anterior and posterior cardinal teeth, with anterior and posterior cardinal sockets. *Goniocardium*'s shell shape (Figs. 24A, 32B) is not unlike that of a typical cockle. However, the anterior part of the hinge is almost entirely lost. A small knob is all that remains of the anterior laterals (*contra* Keen, 1969b), and the anterior lateral socket is continuous with the anterior cardinal socket. The anterior adductor muscle is positioned more anteriorly, closer to the margin of the shell and the posterior adductor muscle is positioned slightly more forward than in *Cerastoderma. Avicularium* (Fig. 32C; Yonge, 1953b, 1981) loses the remnants of the anterior laterals and anterior lateral socket. The posterior adductor scar is enlarged and is more centrally located than in *Goniocardium.* Also, the anterior adductor scar is smaller and more anteriorly located than in *Goniocardium.* In *Byssocardium*, the anterior cardinal tooth is lost, as is the anterior adductor (Fig. 32D). The posterior adductor is larger than in *Avicularium,* and it is centrally

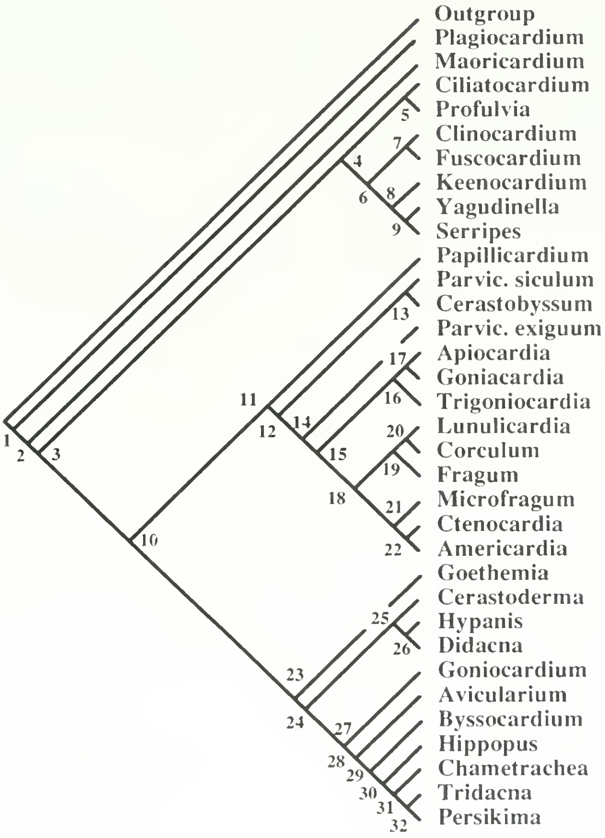

FIG. 34. Tree number 15 (of 28). Synapomorphies for each numbered node indicated in Table 2.

TABLE 3. Shell shape character states detected during ontogeny of species considered in the present analysis. Shell shapes are listed in order of ontogenetic appearance.

Schedocardia hatchetigbeense: circular, schediform (Schneider, 1998).
Plagiocardium granulosum: circular, oval (Schneider, 1998)
Maoricardium pseudolatum: circular, oval, unnamed autapomorphic state
Ciliatocardium ciliatum, Clinocardium nuttallii, Clinocardium (*Fuscocardium*) *braunsi, Clinocardium* (*Keenocardium*) *blandum, Yagudinella notabile, Serripes groenlandicus, Papillicardium papillosum:* circular, oval
Profulvia harrimani: circular, oval, unnamed autapomorphic state
Parvicardium (*Parvicardium*) *siculum, P.* (*P.*) *exiguum, P.* (*Cerastobyssum*) *hauniense, Trigoniocardia* (*Trigoniocardia*) *antillarum, T.* (*Apiocardia*) *obovale, T.* (*Goniacardia*) *callopleura, Goniocardium rachitis:* oval, trigonal
Lunulicardia retusa, Corculum cardissa, Fragum fragum, Avicularium aviculare, Byssocardium emarginatum: trigonal
Microfragum festivum, Ctenocardia (*Ctenocardia*) *symbolica, C.* (*Americardia*) *media:* trigonal, quadrate-short
Goethemia elegantula, Cerastoderma edule: oval, cerastiform
Monodacna (*Hypanis*) *colorata:* oval, cerastiform, hypaniform
Hippopus hippopus, Tridacna (*Chametrachea*) *maxima, Tridacna* (*Tridacna*) *gigas, Tridacna* (*Persikima*) *derasa:* trigonal, unnamed terminal autapomorphy

TABLE 4. Suggested taxonomy of the taxa *Plagiocardium, Maoricardium,* Clinocardiinae, Fraginae, *Goethemia*, Lymnocardiinae, and Tridacninae, based on the present phylogenetic analysis. Stratigraphic ranges from J. J. Sepkoski Jr.'s unpublished compendium of stratigraphic ranges of marine invertebrates, except where indicated. Abbreviations of stratigraphic units from Harland et al. (1990).

Family Cardiidae	Stratigraphic Range
No subfamilial designation	
Plagiocardium	Dan-Mio
Maoricardium	Cht-Hol
Goethemia	Ple-Hol (herein)
Subfamily Clinocardiinae	
Clinocardium	
(*Clinocardium*)	Cht-Hol
(*Fuscocardium*)	Srv-Ple (Kafanov, 1980)
(*Keenocardium*)	Cht-Hol
Ciliatocardium	Rup-Hol
Profulvia	Oli-Ple (Keen, 1980; Kafanov, 1980; Akamatsu & Suzuki, 1990)
Serripes	Rup-Hol
Yagudinella	Srv-Hol (Kafanov, 1980)
Subfamily Fraginae	
Papillicardium	Eoc-Hol
Parvicardium	
(*Parvicardium*)	Ypr-Hol
(*Cerastobyssum*)	Hol (herein)
Trigoniocardia	
(*Trigoniocardia*)	Cht-Hol
(*Apiocardia*)	Pli-Hol
(*Goniacardia*)	Mio-Zan (herein)
Corculum	Pia-Hol (Paulay, 1996)
Lunulicardia	Ple-Hol
Fragum	Mio-Hol (Keen, 1980)
Ctenocardia	
(*Ctenocardia*)	Mio-Hol
(*Americardia*)	Mio-Hol (Keen, 1980)
(*Microfragum*)	Ple-Hol (herein)
Subfamily Lymnocardiinae	
Cerastoderma	Rup-Hol (Keen, 1980)
Hypanis (*Monodacna*)	Zan-Hol (Keen, 1969a)
Didacna (*Didacna*)	Hol (Keen, 1969a)
Subfamily Tridacninae	
Tridacna	
(*Tridacna*)	Aqu-Hol (Rosewater, 1965; Keen, 1969b)
(*Chametrachea*)	Tor-Hol (Rosewater, 1965)
(*Persikima*)	U. Mio.-Hol (Beets, 1986)
Avicularium	Lut-Rup
Byssocardium	Lut-Bur
Goniocardium	Lut-Rup (herein)
Hippopus	Aqu-Hol (Rosewater, 1965)

located. The hinge and arrangement of the muscle scars in Recent giant clams is similar to that of *Byssocardium*.

Early in ontogeny, modern giant clams do have both anterior and posterior adductor muscles and are trigonal in shape (LaBarbera, 1974, 1975; Jameson, 1976; Rosewater, 1981; Fig. 35). Juveniles of *Tridacna* (*Chametrachea*) *maxima* (Röding, 1798) and *T.* (*C.*) *squamosa* Lamarck, 1819, have hinges with anterior lateral and anterior cardinal teeth, which are lost during ontogeny (LaBarbera, 1975). During ontogeny, the anterior adductor muscle becomes smaller and

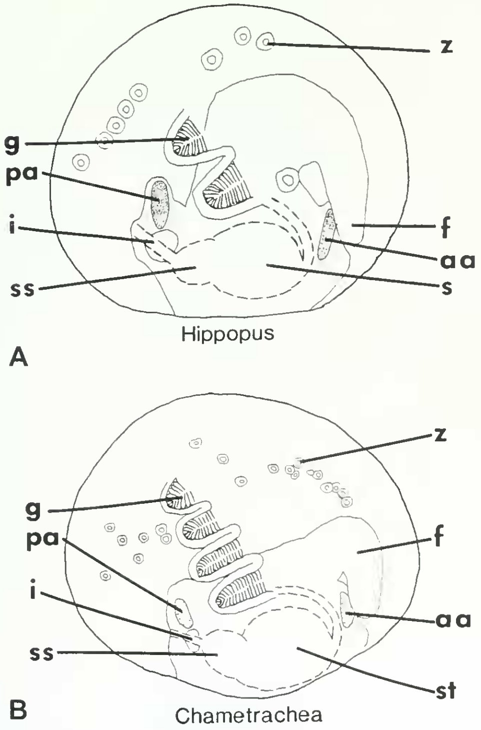

FIG. 35. Tridacnine juveniles. A, 27-day juvenile of *Hippopus hippopus*. Scale bar equals 50 microns. B, 47-day juvenile of *Tridacna* (*Chametrachea*) *maxima*. Scale bar equals 100 microns. From Jameson (1976).

more anterior until it is lost entirely, and the posterior adductor becomes larger and more centrally located. Likewise, through ontogeny, the posterior retractor becomes larger and situated more towards the middle of the shell.

In dimyarian bivalves, including cardiids, length is measured along a line parallel to the line that goes through the midpoint of the adductor muscles (Keen, 1980). Length is measured from the anteriormost point of the shell to the posteriormost shell point along that line (Schneider, 1995, 1998). Because it takes two points to constitute a line, then *Byssocardium* and Recent giant clams have no length. The anterior adductor muscle, along with the rest of the anterior portion of the shell, is absent. Lacking length, at least in the sense homologous to other cardiids, the shells of the giant clams cannot be measured and placed in the shell shape character-state tree (character 31). However, since their juvenile shells do have both adductor muscles, the shape of their juvenile shells can be entered in the shell shape character state tree. Then, as with *Maoricardium* and *Profulvia,* their terminal adult shell shape can be considered as an uncoded autapomorphy. Because extant giant clams lack a length measure, it was decided to code character 1, labial palp length, as missing.

Stasek (1962) reviewed the controversy regarding the ontogeny and morphology of giant clams. Vaillant (1865) proposed the idea that the animal has rotated relative to the mantle and shell and was followed by Dall (1895), Grobben (1898), and Keen (1969b). The concept of rotation was rejected by Lacaze-Duthiers (1902), Anthony (1904, 1920), Pelseneer (1911), and Boutan (1919). Instead, these authors felt that the tridacnid form was a result of differential growth: a tremendous rate of growth of the posterior portions of the animal and shell, and essentially no growth (or even negative growth; i.e., shell resorption) of the anterior portion of the shell. However, Yonge (1936) proposed that in the evolution of giant clams, the shell and mantle had rotated about the animal. Most later studies (Mansour, 1946; Yonge, 1953b, 1981; Purchon, 1955; Rosewater, 1965; Seilacher, 1990; Janssen, 1992; Schneider, 1992) accepted Yonge's thesis. Only Stasek (1962) and LaBarbera (1975) supported the concept of differential growth as responsible for the ontogenetic and evolutionary patterns of giant clams.

From character analysis, ontogeny, and subsequent phylogenetic analysis, it appears that the evolution of giant clam form does not involve rotation, but differential growth. Specifically, giant clams seem to lack almost the entire front half of the shell (the anterior anatomical features, such as the mouth, labial palps, and ctenidia remain essentially the same as in *Cerastoderma;* Yonge, 1953b). In the evolution of giant clams, the posterior part of the shell grew in an increasingly rapid pace relative to the front half of the shell, which essentially stops growing after the settlement of the planktotrophic larva. Stasek (1962) plotted the relative proportions of homologous regions of the mantle/shell of the *Clinocardium nuttallii* (Conrad, 1837) and *Tridacna* (*Chametrachea*) *maxima* (Fig. 36). The anterior shell region is absent on *T. maxima*. Because the Recent giant clams lack the anterior portion of the shell, they are coded as missing (?) for degree of umbonal prosogyry (character 29), for

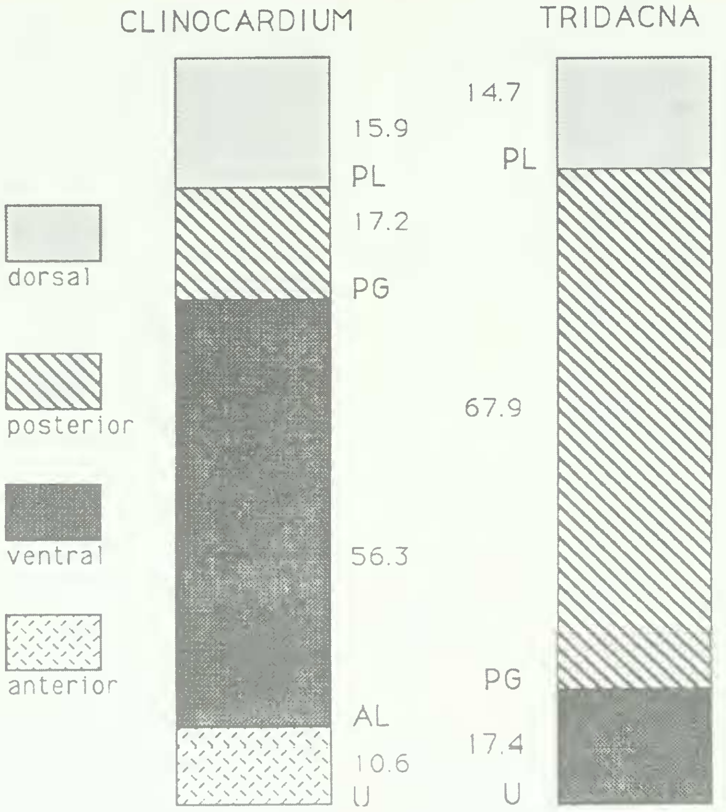

FIG. 36. Relative proportions of homologous regions of mantle/shell and relative distribution of marginal increments about the perimeter of *Clinocardium nuttallii* and *Tridacna* (*Chametrachea*) *maxima*. Numbers indicate percent of total perimeter for a particular region. From Stasek (1962).

there is no anterior direction into which the beaks can be pointing.

In regards to the hinge and the adductor and pedal retractor muscles, the evolution of giant clams is a case of peramorphosis. The ontogeny of these structures in the juveniles of modern giant clams recapitulates the states of these characters in concordance with the pattern of phylogenetic relationships of the group: (*Goniocardium* (*Avicularium* (*Byssocardium* (*Hippopus* (*Tridacna*))))). Yonge (1936, 1981) had thought that it was impossible for the ontogeny of giant clams to recapitulate their phylogeny.

In contrast to the peramorphosis of the shell and of the adductor and retractor muscles, the byssus of giant clams is paedomorphically retained late into ontogeny. The byssus, present in all or most larval cardiids (Pelseneer, 1911; Yonge, 1936), is retained throughout adulthood in *Chametrachea* (Rosewater, 1965; Yonge, 1953b, 1981; Lucas et al., 1991; pers. obs.). Other tridacnines are byssally attached early in ontogeny but later become free-living and the byssus is lost (Rosewater, 1965; Yonge, 1953b, 1981; Lucas et al., 1991). Because of the tremendous increase in both growth rate and size attributable to photosymbionts, it is difficult to ascertain the result of the paedomorphic processes responsible for the retention of the byssus in tridacnines. It should be noted that *Avicularium* and *Byssocardium* have byssal gapes (Schneider, 1998), but these shells are not notably large. The tremendous size increase in tridacnines may not have occurred until the Miocene origination of the Recent taxa. Ironically, this size increase is thought to be responsible for the subsequent *loss* of the byssus and byssal gapes in the adults of *Tridacna, Persikima, Hippopus,* and very large specimens of *T.* (*Chametrachea*) *squamosa,* for these large clams are held in place simply by their bulk (Rosewater, 1965; Yonge, 1953b, 1981; Lucas et al., 1991).

Goniocardium lacks a byssal gape (Schneider, 1998). A narrow byssal gape is present throughout ontogeny in *Avicularium;* a wider byssal gape is present throughout ontogeny in the more derived *Byssocardium* and *Chametrachea* (Schneider, 1998; Fig. 27A). The closing of the byssal gape throughout post-juvenile ontogeny can be seen in the shells of *Hippopus, Tridacna,* and to a lesser degree, *Persikima* (Rosewater, 1965; Yonge, 1981; Figs. 25, 29, 30). The closing of the byssal gape (and subsequent loss of byssus) is a peramorphic superimposition onto the paedomorphic retention of the byssus into post-larval development. Heterochrony resulting in pre-displacement is responsible for the closing of the byssal gape, for the descendant adult morphology has developed beyond that of its ancestor (McNamara, 1986).

Independently, fragines also paedomorphically retain the byssus into adulthood. In this instance, heterochrony results in post-displacement, for an ancestral juvenile character (functional byssus) is present in the adult, without the size increase found in neoteny. In the present analysis, it is hypothesized that Fraginae and Tridacninae independently derived a functional byssus in the adult.

Morton (1988) noted that the foot is reduced in cemented or unusually inactive bivalves. The tridacnines are sedentary nonburrowers (Rosewater, 1965; Yorge, 1981): *Chametrachea* byssally attaches to, or bores into, hard substrata. *Tridacna* and *Perskima* are likewise byssally attached to hard substrata early in life; late in ontogeny the byssal apparatus is lost and they are epifaunal on hard substrata. *Hippopus* is epifaunal on sandy surfaces. The fragine clades *Parvicardium* + *Cerastobyssum* and *Corculum* independently lose the ventral ridge. Fragines, especially *Corculum,* are the most superficial burrowers of the non-tridacnine cardiids (Stanley, 1970; Savazzi, 1985; Severin & Cooper, 1989).

In the evolution of Cenozoic eucardiids from their Cretaceous ancestor, adjacent ribs fused together, forming one wide rib (Schneider, 1993a, 1998). A single rib on a Cenozoic eucardiid is homologous to two ribs on a Cretaceous eucardiid. The Maastrichtian *Perucardia* displays an intermediate condition. The anterior and posterior slopes of the shell of *Perucardia* have ribs as on Cretaceous eucardiids, whereas the central slope has the fused ribs of Cenozoic eucardiids.

Study of the ontogeny and phylogenetic relationships of tridacnines indicates that rib reduction in this group has proceeded by a process which can be called rib suppression. The radial ribs of *Goniocardium, Avicularium,* and *Byssocardium* are all of the same strength and width over the entire surface of the shell. Each rib will bear only one row of scutes (Fig. 24). On the most basal living tridacnine, *Hippopus,* the "primary" ribs (terminology of Rosewater, 1965) are homologous to several radial ribs, and indeed they may bear multiple rows of scutes (Fig. 25). Rosewater termed these multiple "secondary" ribs as "riblets." Riblets are also present in between the primary ribs. On *Chametrachea,* the riblets are apparent throughout ontogeny (Rosewater, 1965; Fig. 26). The underside of the "primary" ribs of *Hippopus* and *Chametrachea* has several marginal serrations (Figs. 25, 26); each marginal serration corresponds to a riblet and is homologous to one rib on *Goniocardium, Avicularium,* and *Byssocardium.* On the more derived *Tridacna* and *Persikima,* the riblets are readily apparent only early in ontogeny (Figs. 28–31). Only the riblets of *Hippopus* bear scutes (Fig. 25). Rosewater's "riblets" are homologous to radial ribs, whilst his "primary" ribs are secondary undulations in the commissure superimposed over the primitive and suppressed cardiid radial rib pattern.

Photosymbiosis in Cardiids

All species of tridacnines are known to harbor photosymbiotic dinoflagellate algae (zooxanthellae) in their tissues (Trench et al., 1981; Alcazar et al., 1987; Lucas et al., 1991). Photosymbiotic dinoflagellates have also been found in the fragines *Corculum cardissa* (Linné, 1758), *Lunulicardia retusa* (Linné, 1767), *Fragum fragum* (Linné, 1758), *F. unedo* (Linné, 1758), *F. mundum* (Reeve, 1845), *F. loochooanum* Kira, 1962, and two undescribed species of *Fragum* (Kawaguti, 1950, 1968, 1983; Trench et al., 1981; Umeshita & Yamasu, 1985; Yamasu, 1988a, b; Severin & Cooper, 1989; Paulay, 1996.; pers. obs.). These photosymbionts transfer excess carbon from photosynthesis to the host's tissues (Trench et al., 1981; Fisher et al., 1985, Klumpp et al., 1992).

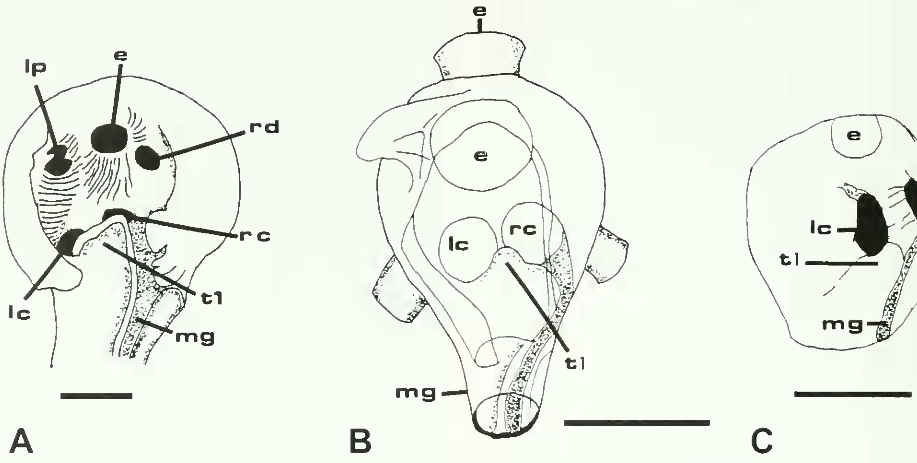

FIG. 37. Representative stomachs of lucinoids. A, *Diplodonta semiaspera* (Ungulinidae). B, *Thyasira flexuosa* (Thyasiridae). C, *Loripes lucinalis* (Lucinidae). Note following structures: GT, major typhlosole; LC, left caecum; RC, right caecum. Lucinids lack a right caecum. All scales = 1 mm. From Allen (1958).

Bivalves of the families Lucinidae and Solemyidae (as well as members of several other families) have chemautotrophic bacteria in their tissues (Reid, 1990); this phenomenon is known as chemosymbiosis. Lucinids reduce and/or lose many of the structures in their digestive system (Allen, 1958; Reid, 1990; CoBabe, 1991; Fig. 37). The stomach and the gut are reduced or even lost, and the labial palps and the outer demibranch are lost. Simplification of the stomach involves reduction from the typical type V stomach to a type IVb stomach (Purchon, 1960a, 1987a). In type V stomachs, the major typhlosole emerges from the midgut, enters the right caecum, then reemerges and traverses across the floor of the stomach, before finally entering the left caecum. In a type IV stomach, the major typhlosole simply emerges from the midgut, crosses the floor of the stomach and enters the left caecum. The major typhlosole does not enter the right caecum.

Solemyids reduce or lose the gut (Morse, 1913; Yonge, 1939; Owen, 1961; Reid 1980, 1990; Reid & Bernard, 1980; Kuznetsov & Shileiko, 1984), as well as the esophagus (Reid & Bernard, 1980; Reid, 1990). In both lucinids and solemyoids, the chemosymbionts provide all or most of the nutrition for the clam (Conway et al., 1989; Conway & McDowell Capuzzo, 1991; Fisher & Childress, 1986; Reid, 1990; Krueger et al., 1992).

Primitively, eucardiids have a very long and complex gut, as seen in *Acanthocardia*, *Maoricardium,* and the Clinocardiinae (Figs. 9, 10A). This type of gut (13:3) exits from the style sac and loops eleven times before exiting the visceral mass and terminating at the anus. *Acanthocardia*, *Maoricardium* and the Clinocardiinae have the typical cardiid type V stomach (Graham, 1949; Purchon, 1960a, 1987a; Nakazima, 1964b; Fig. 11). The major typhlosole emerges from the midgut, going first to the right caecum and then to the left caecum.

Clinocardiines have always been restricted to the cool temperate and arctic waters of the northern hemisphere, especially from Oregon north to Alaska (Kafanov, 1980), a zone of upwelling (Berger, 1989). High latitude and otherwise cool waters generally have higher productivity than warmer, low latitude waters (Berger, 1989). Therefore, it is not unexpected to find that the clinocardiine digestive system, is at least as complex, or even more complex, than those of *Acanthocardia* (North Atlantic and Mediterranean) and *Maoricardium* (Indo-Pacific), which live in areas of lower productivity. Modifications of the clinocardiine digestive tract include the presence of (1) an additional typhlosole on the right posterior portion of the stomach (17:1) in *Ciliatocardium* and *Serripes,* (2) a raised bar running across the middle of the stomach (19:1) in *Clinocardium, Keenocardium,* and *Serripes,* and (3) a food groove on the outer demibranch of *Serripes groenlandicus* (Fig. 5B). The other Recent species of *Serripes, S.*

laperousii (Deshayes, 1839), lacks a food groove on the outer demibranch (pers. obs.).

Papillicardium is the most basal fragine and has a gut and stomach similar to that of *Maoricardium*. However, the labial palps are reduced (1:0), as in the chemosymbiont-bearing lucinoideans and solemyoideans. *Parvicardium siculum* (Figs. 10C, 11H) has a similar stomach but has reduced the gut. Neither *Cerastobyssum* (the sister taxon to *P. siculum*) nor *P. exiguum* have reduced guts.

In *Apiocardia* and *Trigoniocardia*, the stomach has been simplified from a type V stomach to a type IV stomach. The midgut/style sac opening is not located posteriorly, but anteriorly. The major typhlosole goes directly from the midgut/style sac opening to the left caecum. This is the first report of a type IV stomach in Cardiidae. *Apiocardia* undergoes a reversal to the primitive states of a complex gut (13:4) and large labial palps (1:1). *Lunulicardia* also undergoes reversals of digestive characters: large labial palps (1:1) and a posteriorly located midgut/style sac opening (18:0). *Lunulicardia* and *Corculum* have a simplified stomach, but not as in *Apiocardia* and *Trigoniocardia*. The major typhlosole enters only one caecum, but it is the right caecum, not the left caecum. Functionally, the stomach of *Lunulicardia* and *Corculum* is a type IV stomach, although it does not adhere to Purchon's (1960a, 1987a) definition of a type IV stomach. *Fragum* and the *Ctenocardia*-group have a type V stomach, although the style sac is located anteriorly. Other simplifications of the digestive system of these cardiids are the reduction of the crystalline style and style sac of *Corculum* and the loss of ridges on the labial palps of *Microfragum* (Fig. 3B).

Reduction of digestive structures is often indicative of symbiosis with microorganisms. Bernard (1980) and Kuznetsov & Shileiko (1984) have inferred symbiosis in some solemyids and nucinellids because these bivalves are gutless (reviewed by Reid, 1990). Of the fragines that significantly simplify their digestive system, only *Microfragum*, *Fragum*, *Lunulicardia* and *Corculum* have been the subject of any sort of anatomical investigation previous to Schneider (1992) and this study (Pelseneer, 1911; Kawaguti, 1950, 1968, 1983; Kratzing & Ladd, 1967; Matsuno, 1988; Severin & Cooper, 1989; Janssen, 1991, 1992; Ohno et al., 1995). It is not that *Apiocardia*, *Trigoniocardia*, *Americardia*, and *Ctenocardia* have been found to lack photosymbionts; it is that no one has ever examined the soft parts of species of these taxa. Based on the reduction of the stomach and intestine, it is predicted that all or most of the species of these four taxa harbor photosymbiotic dinoflagellates in their tissues. However, Ohno et al. (1995) report that *Microfragum festivum* (Deshayes, 1854) lacks photosymbionts.

Giant clams, which are well known for bearing symbiotic dinoflagellates in their tissues (Brock, 1888; Bochsma, 1924; Yonge, 1936, 1981; Rosewater, 1965; Trench et al., 1981; Klumpp et al., 1992; numerous others), have a fully functional digestive system (Trench, 1974; Morton, 1978; Reid et al., 1984). Tridacnines do not simplify the stomach, except for the loss of the esophageal sorting area (21:1). However, the stomach of giant clams does have a ridge (20:1), and the major typhlosole forms a tight spiral on the floor of the stomach (14:0). The gut is somewhat reduced (13:2); however, this character state is shared with lymnocardiines and should not be interpreted as having been derived as a result of the acquisition of zooxanthellae. Additionally, the largest species of giant clam, *Tridacna gigas*, develops a food groove on its outer demibranch (4:1). The clinocardiine *Serripes groenlandicus* is the only other cardiid known to have a food groove on its outer demibranch. Furthermore, Yonge (1932, 1936) reported that the crystalline style and style sac is unusually large in *Tridacna* (*Persikima*) *derasa*.

Tridacnines include the largest and fastest-growing Recent bivalves (Bonham, 1965; Yonge, 1981; Klumpp et al., 1992). Bonham suggested that the shell of *Tridacna gigas* (the largest of the giant clams; Rosewater, 1965) increases in thickness by 1 cm annually. Yonge (1981) reported that a specimen of *T. gigas* grew to a length of 55 cm in about six years. Klumpp et al. (1992) reported that *T. gigas* grew from 1.7 cm to 19 cm in 28 months. It has been found that photosymbionts can potentially satisfy all the respiratory requirements of giant clams (Gwyther & Munro, 1981; Fisher et al., 1985; Klumpp et al., 1992). The photosymbionts augment a fully functional digestive system; hence the spectacular growth rates and size of giant clams.

The present results indicate that symbiosis with dinoflagellate algae evolved separately in Tridacninae and Fraginae. Kawaguti (1983) had suggested that photosymbiosis evolved only once. If Tridacninae and Fraginae are posited as sister taxa, tree length increases by five steps. It is felt that the present results reject the hypothesis that symbiosis with dinoflagellate algae evolved only once in cardiids.

Goethemia independently simplifies its gut (13:0). Given its subarctic distribution (Clench & Smith, 1944; Voskuil & Onverwagt, 1989), it is unlikely to bear photosymbionts. *Goethemia* never is larger than 14 mm, and the simplification of the gut may simply be a consequence of the increase of the surface area/volume ratio (Reid & Bernard, 1980).

Some populations of the clinocardiine *Clinocardium nuttallii* from Oregon and Washington have a very different sort of alga in their tissues. Cooke (1975) and Hartmann & Pratt (1976) independently reported the presence of a zoochlorella of the form genus *Chlorella* in the tissues of *C. nuttallii*. Hartmann & Pratt (1976) and Jones & Jacobs (1992) reported that algae are absent in small, young, infaunal individuals. Larger and older semi-infaunal clams contain algae only in tissues exposed to sunlight (Jones & Jacobs, 1992). Finally, the oldest, largest, epifaunal clams have algae throughout the mantle and foot tissues. This is in contrast to the dinoflagellate algae in tridacnines, which are ingested by the clams during the veliger stage or early juvenile stage (LaBarbera, 1975; Jameson, 1976; Fitt & Trench, 1981). Hartman & Pratt considered the zoochlorella to be parasitic on *C. nuttallii*, but Jones & Jacobs suggested that *C. nuttallii* is at an intermediate stage of evolving a symbiotic relationship with the zoochlorella. If this is true, then *C. nuttallii* has not yet reached the stage at which reduction of the digestive system occurs (this stage was never reached in tridacnines). The amount of carbon, if any, that the zoochlorellae contribute to *C. nuttallii* is still unknown.

Phylogeny and the Fossil Record

The results of the phylogenetic analysis are broadly concordant with the fossil record (Fig. 38). *Plagiocardium* appears in the Paleocene (Keen, 1980). The oldest known clinocardiines are Early Oligocene (Kafanov, 1980; Kafanov & Savitskiy, 1982). *Papillicardium*, the most basal fragine, originates in the Eocene (Keen, 1980; Schneider, 1993a, 1998). *Parvicardium* also originates in the Eocene (Keen, 1980; Schneider 1993a, 1998).

Goethemia as the sister taxon to Tridacninae + Lymnocardiinae is the only notable stratigraphic anomaly (within a particular clade, a case of a more derived taxon appearing before a less derived taxon) in the present phylogenetic analysis. *Goethemia*'s fossil record dates from the earliest Pleistocene, whereas the three extinct tridacnine taxa are known from the Middle Eocene, and the extant tridacnine taxa are known from Miocene fossils. The oldest lymnocardiine fossils are Early Oligocene (Keen, 1969a, 1980). *Goethemia* is known from its Recent type species, *Cardium elegantulum* Möller, 1842 (*ex* Beck MS). I would also place *Cardium strigilliferum* Wood, 1853, from the lowermost Pleistocene Red Crag of England, in *Goethemia*. If the results of the present phylogenetic analysis are accepted, then *Goethemia* would be hypothesized to have originated in the Eocene.

A minor stratigraphic anomaly is *Microfragum*. *Microfragum*'s fossil record consists only of Pleistocene specimens of *Cardium ebaranum* (discussed in Materials and Methods). If we were to accept the results of the ordered analysis, *Microfragum* is the sister taxon to *Ctenocardia* + *Americardia*, and *Microfragum* is postulated to have originated in the Miocene.

Valentine (1989) found that 77% of Recent bivalve and gastropod species of the California Province are known from Pleistocene fossils. Those forms that have yet to be found as fossil are fragile, minute, and rare, although rare forms are found as new studies are conducted. *Goethemia* and *Microfragum* fulfill all three of these criteria: they are small (*Goethemia* no larger than 14 mm long; *Microfragum* less than 15 mm high), fragile, and rare (Clench & Smith, 1944; Keen, 1980; Voskuil & Onverwagt, 1989). Additionally, *Goethemia* lives in an area (boreal Atlantic Ocean: Massachusetts north to Baffin Bay, west Greenland, Iceland, northern and western Norway, Spitsbergen, Barents Sea; Fischer-Piette, 1977) for which there was virtually no net marine sedimentation during the Cenozoic until the Pliocene. To my knowledge, *Goethemia* is absent from the few Pliocene and Pleistocene localities in New England, eastern Canada, Greenland, and Iceland. Given its low preservation potential, *Goethemia*'s absence from the fossil record, from a cladisticially postulated Eocene origin until the Pliocene, is plausible. The phylogenetic position of *Goethemia* as the sister taxon to Tridacninae + Lymnocardiinae should not be rejected simply on the basis of the fossil record.

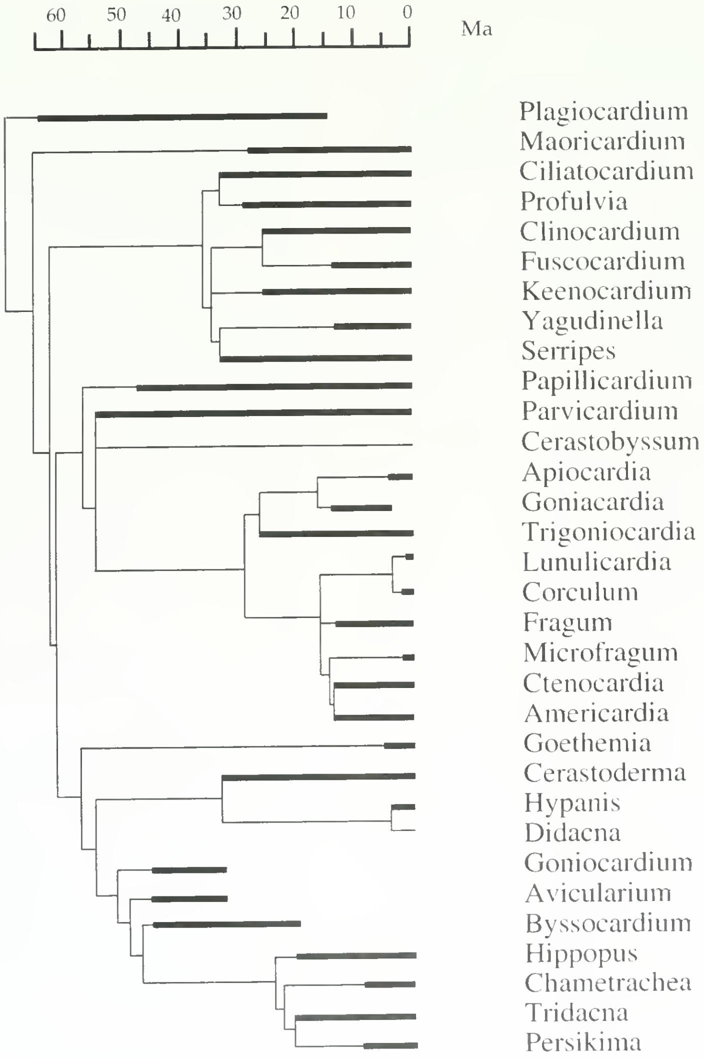

FIG. 38. Phylogenetic results of the ordered analysis plotted against the fossil record. Time scale from Harland et al. (1990). Stratigraphic ranges from Table 3. *Parvicardium* is represented only once, with earliest species known from the Eocene (see text; Schneider 1998). Taxa with no fossil record indicated by narrow horizontal line at 0 Ma.

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APPENDIX 1

Material examined. Number of specimens examined indicated in parentheses.

Acanthocardia aculeata (Linné, 1758). USNM 304723 (4); ANSP 54235 (12); UNC 15376 (2). Anatomical: NHM Acc. 2322 (1).

Acanthocardia (Schedocardia) hatchetigbeense (Aldrich, 1886). USNM 645087 (1, syntype), 638802 (1, syntype); ANSP 5420 (1), 8687 (1), 8756 (3).

Plagiocardium granulosum (Lamarck, 1805). ANSP 6268 (14), 7663 (1).

Maoricardium pseudolatum Voskuil & Onverwagt, 1991. ANSP A103 (55); AM C.164058 (3). Anatomical: AM C.164058 (3).

Ciliatocardium ciliatum (Fabricius, 1780). ANSP 54269 (12), FMNH 278012 (1). Anatomical: USNM 600831 (4), 604850 (3), 796257 (11); ANSP 64388 (1); FMNH 278012 (1).

Profulvia harrimani (Dall, 1904). USNM 164867 (1) (holotype); UCMP A-22582 (1).

Clinocardium nuttallii (Conrad, 1837). Shell: YPM 10148 (1), 10149 (1). Shell and anatomy: FMNH 49126 (1), 278015 (2), 278016 (1).

Clinocardium (Fuscocardium) braunsi (Tokunaga, 1906). Data from Oyama (1973).

Clinocardium (Keenocardium) blandum (Gould, 1850). USNM 3899 (1), 304266 (1); FMNH 12851 (2); ANSP 85407 (2). Anatomical: FMNH 12581 (2). Misidentified as *Clinocardium (Keenocardium) californiense* (Deshayes, 1839) by Schneider (1993b).

Serripes groenlandicus (Mohr, 1786). ANSP 64421 (11), FMNH 278013 (2); YPM 49159 (1). Anatomical: USNM 600836 (1), 604849 (2), 796460 (2); FMNH 278013 (2).

Yagudinella notabile (Sowerby, 1915). FMNH 278014 (1).

Papillicardium papillosum (Poli, 1795). AMNH 29980 (3), 29981 (4); ANSP 54098 (1), 54266 (13). Anatomical: MNHN, unnumbered specimens (18).

Parvicardium siculum (Sowerby, 1841). ANSP 54123 (1), 54266 (1), 54288 (1), 54289 (9); AMNH 226511 (1). Anatomical: AMNH 226511 (1), 226512 (3).

Parvicardium exiguum (Gmelin, 1791). ANSP 54121 (4), 209588 (1); USNM 171808 (1); NHM 1964269W (50). Anatomical: NHM 1964269W (50).

Parvicardium (Cerastobyssum) hauniense Petersen & Russell, 1971. Conchological and anatomical: ZM, unnumbered specimens (3).

Trigoniocardia antillarum (Orbigny, in Ramon de la Sagra, 1842). ANSP 54283 (60), 283822 (22); USNM 429926 (2). Anatomical: USNM 857540 (2).

Trigoniocardia (Apiocardia) obovale (Sowerby, 1833). AMNH 78213 (19), 72589 (11), 78218 (9); ANSP 317706 (51). Anatomical: ANSP 316937 (2); 81974 (1).

Trigoniocardia (*Goniacardia*) *callopleura* Gabb, 1881. ANSP 3439 (2, syntypes), 3445 (2).

Lunulicardia retusa (Linné, 1767). AMNH 30073 (21); ANSP 12527 (4), 302424 (12), 319313 (2); USNM 631219 (2); YPM 9676 (1). Anatomical: ANSP 302424 (1).

Corculum cardissa (Linné, 1758). ANSP 231526 (40); UNC 8291 (1); USNM 636206 (2). Anatomical: ANSP 200771 (1); USNM 661032 (1).

Fragum fragum (Linné, 1758). ANSP 288688 (68); USNM 674681 (2). Anatomical: ANSP 289145 (9); USNM 746995 (1), 747674 (1), 766795 (1), 849695 (1).

Ctenocardia symbolica Iredale, 1929. ANSP 229980 (10); USNM 236040 (2). Anatomical: ANSP 229873 (2).

Ctenocardia (*Americardia*) *media* (Linné, 1758). ANSP 54280 (14); PRI 26699 (2), 33068 (1); USNM 92089 (2), 36431 (2). Anatomical: NHM Acc. No. 2270 (6); ANSP 297243 (2); USNM 801849 (1), 801850 (1), 804669 (1), 847861 (1).

Microfragum festivum (Deshayes, 1854). ANSP 54263 (4). Conchological and anatomical: AM C.164061 (4), C.164062 (10).

Goethemia elegantula (Möller, 1842, *ex* Beck MS). Conchological and anatomical: SMNH 883 (6), 1482 (6); NHM 196284W (6); ZM, unnumbered specimens (3).

Cerastoderma edule (Linné, 1758). ANSP 54252 (15); FMNH 278010 (2); YPM 9672 (1). Conchological and anatomical: NHM 1964273W (17); FMNH 278010 (2), 278017 (2); UMMZ, unnumbered specimens (3).

Hypanis (*Monodacna*) *colorata* (Eichwald, 1829). ANSP 338065 (25). Anatomical: USNM 769939 (2).

Didacna trigonoides (Pallas, 1771). ANSP 54193 (4). Anatomical: NHM 1862.11.19.33 (2).

Goniocardium rachitis (Deshayes, 1829). ANSP 12429 (6); FMNH PE 3624 (2).

Avicularium avicularium (Lamarck, 1805). ANSP 6279 (3).

Byssocardium emarginatum (Deshayes, 1829). IRSNB I. G. 10591 (4).

Hippopus hippopus (Linné, 1758). FMNH 2635 (1), 164189 (1); USNM 63793 (6). Anatomical: UMMZ, 265468 (1).

Tridacna (*Chametrachea*) *maxima* Röding, 1798. FMNH 156836 (2); ANSP 252683 (2), 269769 (1). Anatomical: ANSP A3276 (1); UMMZ 265463 (1).

Tridacna gigas (Linné, 1758). USNM 602502 (2), 686575 (4). Anatomical: UMMZ 265466 (1).

Tridacna (*Persikima*) *derasa* Röding, 1798. USNM 654256 (4), 845538 (40). Anatomical: UMMZ 265467 (1).

APPENDIX 2

Abbreviations of Repositories

AM: Australian Museum, Sydney, Australia.

AMNH: American Museum of Natural History, New York, New York, USA

ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.

FMNH: Field Museum of Natural History, Chicago, Illinois, USA.

GSI: Geological Survey of India, Calcutta, India.

IRSNB: Institut Royal des Sciences Natuelles de Belgique, Brussels, Belgium.

MACSRI: Mahrashtra Association form the Cultivation of Science, Research Institute, Pune, India.

MNHN: Museum National d'Histoire Naturelle, Paris, France.

NHM: The Natural History Museum. London, United Kingdom.

PRI: Paleontological Research Institution, Ithaca, New York, USA.

SMNH: Swedish Museum of Natural History, Stockholm, Sweden.

UCMP: University of California Museum of Paleontology, Berkeley, California, USA.

UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.

UNC: University of North Carolina, Department of Geology, Chapel Hill, North Carolina, USA.

USNM: United States National Museum, Washington, D.C., USA.

YPM: Yale Peabody Museum, New Haven, Connecticut, USA.

ZM: Zoologisk Museum, Copenhagen, Denmark.

APPENDIX 3

List of Abbreviations

aa	anterior adductor
ac	anterior cardinal
acs	anterior cardinal socket
al	anterior lateral
alid	ascending lamella of inner demibranch

alod	ascending lamella of outer demibranch
als	anterior lateral socket
avl	anterior ventral lateral
bcl	branching crossed-lamellae
bg	byssal gape
by	byssus
cs	cross-striae
dlid	descending lamella of inner demibranch
dlod	descending lamella of outer demibranch
e	esophagus
ea	excurrent aperture
f	foot
fg	food groove
fp	fibrous prisms
g	gill
i	intestine
ia	incurrent aperture
id	inner demibranch
ip	inner palp
lc	left caecum
lf	lunule flap
lg	ligament
lp	labial palp
lpo	left pouch
lr	lateral ridge
n	nymph
od	outer demibranch
og	oral groove
op	outer palp
pa	posterior adductor
pc	posterior cardinal
pci	periostracal cilia
pcs	posterior cardinal socket
pf	periostracal frill
pg	pedal gape
pl	posterior lateral
pls	posterior lateral socket
ps	pseudocarina
pss	perisiphonal suture
r	ridge
rb	raised bar
rbl	riblet
rc	right caecum
rd	right duct
rr	rib
s	spine
sa	supra-axial extension of demibranch
saa	anterior sorting area (SA8)
sae	sorting area of esophagus (SA7)
sap	posterior sorting area (SA3)
sc	scute
sf	spiral fold
sia	siphonal area
ss	style sac
st	stomach
t	tentacle
t1	major typhlosole
t3	tertiary typhlosole
u	umbo
v	valvule
vm	visceral mass
vp	ventral papillae
vr	ventral ridge
z	zooxanthellae

APPENDIX 4

Taxonomy of taxa considered herein by Keen (1980); family Lymnocardiidae and superfamily Tridacnacea from Keen (1969a, b).

- Superfamily Cardiacea
- Family Cardiidae
  - Subfamily Cardiinae
    - *Parvicardium*
    - *Plagiocardium*
      - (*Plagiocardium*)
      - (*Maoricardium*)
      - (*Papillicardium*)
  - Subfamily Fraginae
    - *Fragum*
      - (*Fragum*)
      - (*Lunulicardia*)
    - *Corculum*
    - *Ctenocardia*
      - (*Ctenocardia*)
      - (*Afrocardium*)
      - (*Microfragum*)
    - *Trigoniocardia*
      - (*Trigoniocardia*)
      - (*Americardia*)
      - (*Apiocardia*)
  - Subfamily Laevicardiinae
    - *Cerastoderma*
    - *Clinocardium*
      - (*Clinocardium*)
      - (*Ciliatocardium*)
      - (*Fuscocardium*)
      - ? (*Keenocardium*)
    - *Serripes* (= *Yagudinella*)
    - *Laevicardium* (*Profulvia*)
- Family Lymnocardiidae
    - *Hypanis* (*Monodacna*)
    - *Didacna*
  - Superfamily Tridacnacea
- Family Tridacnidae
    - *Tridacna*
      - (*Tridacna*)
      - (*Chametrachea*)
      - (*Persikima*)

- *Avicularium*
- *Byssocardium*
- *Goniocardium*
- *Hippopus*
- *Sawkinsia*

APPENDIX 5

Taxonomy of taxa considered herein by Popov (1977), with emendations on Clinocardiinae and Lymnocardiinae from Kafanov & Popov (1977) and Kafanov (1980).

- Superfamily Cardioidea
- Family Cardiidae
  - Subfamily Clinocardiinae
    - *Clinocardium*
      - (*Clinocardium*)
      - (*Fuscocardium*)
    - *Ciliatocardium*
    - *Keenocardium*
    - *Profulvia*
    - *Serripes*
    - *Yagudinella*
  - Subfamily Fraginae
    - *Fragum*
      - (*Fragum*)
      - (*Ctenocardia*)
    - *Corculum*
      - (*Corculum*)
      - (*Lunulicardia*)
    - *Trigoniocardia*
      - (*Trigoniocardia*)
      - (*Americardia*)
    - *Plagiocardium*
    - *Maoricardium*
    - *Parvicardium* (= *Papillicardium*)
  - Subfamily Lymnocardiinae
    - *Cerastoderma*
    - *Didacna*
    - *Monodacna*
- Superfamily Tridacnoidea